

IX. *The Araucariæ, Recent and Extinct.*

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Received November 13,—Read December 14, 1905.

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## I. INTRODUCTION.

“The Coniferæ undoubtedly constitute one of the most interesting families in the vegetable kingdom, whether considered in connection with the former vegetation of the earth or in reference to their peculiarities of structure.”\*

These introductory words to a memoir by David Don, published in 1841, are applicable with equal force to the Araucariæ and afford a fitting preface to the present communication.

Palæontological evidence has demonstrated that the Araucariæ are remnants of an ancient stock. It seemed to us desirable to ascertain whether the genera *Araucaria* and *Agathis* exhibit any of those features which are often associated with survivals from the past. Do the existing species furnish any evidence of primitive characters, or do they afford any indications as to the lineage of the Araucarian phylum?

Our object has been to give a general account of the Araucariæ based, as far as possible, on an investigation of actual specimens and amplified by a perusal of the widely-scattered literature concerned with both recent and extinct forms. Our work does not claim to be an exhaustive monograph. There are obvious lacunæ, some of which can be filled in only by those who have access to flowering trees at different seasons; but our object has been gained if we succeed in drawing attention to a somewhat neglected section of Coniferales, which we believe to be of paramount importance as a link in the chain of evidence connected with the phylogeny of the Gymnosperms.

In these days of botanical activity, if we would avoid the danger of too great concentration on points elucidated or suggested by the numerous authors of laboratory researches, it is imperative to take more frequent stock of our knowledge with a view to utilising it as a key to those problems of descent which it is our ultimate aim to solve.

We take this opportunity of expressing our hearty thanks to Sir WILLIAM THISSELTON-DYER, through whose kindness we have been supplied with much of our material, and to Mr. MAIDEN of Sydney, who has sent us reproductive and vegetative shoots of *Araucaria* and *Agathis*. We are indebted also to Dr. LANG, of Glasgow, for some examples of Araucarian ovules.†

In the *Genera Plantarum* of DE JUSSIEU, *Araucaria* appears as one of the six genera included in the ‘*Coniferæ veræ*.’‡ RICHARD’S ‘*Commentatio Botanica de Conifereis et Cycadeis*,’§ contains an interesting *résumé* of the treatment of the Coniferæ by earlier writers; his list of 16 genera is divided into three sections—

\* DON (1841), p. 163.

† I have recently received, through the kindness of Professor TREUB, several cones of *Agathis*, which are now being examined and may serve as the subject of a supplementary note.—A. C. S.

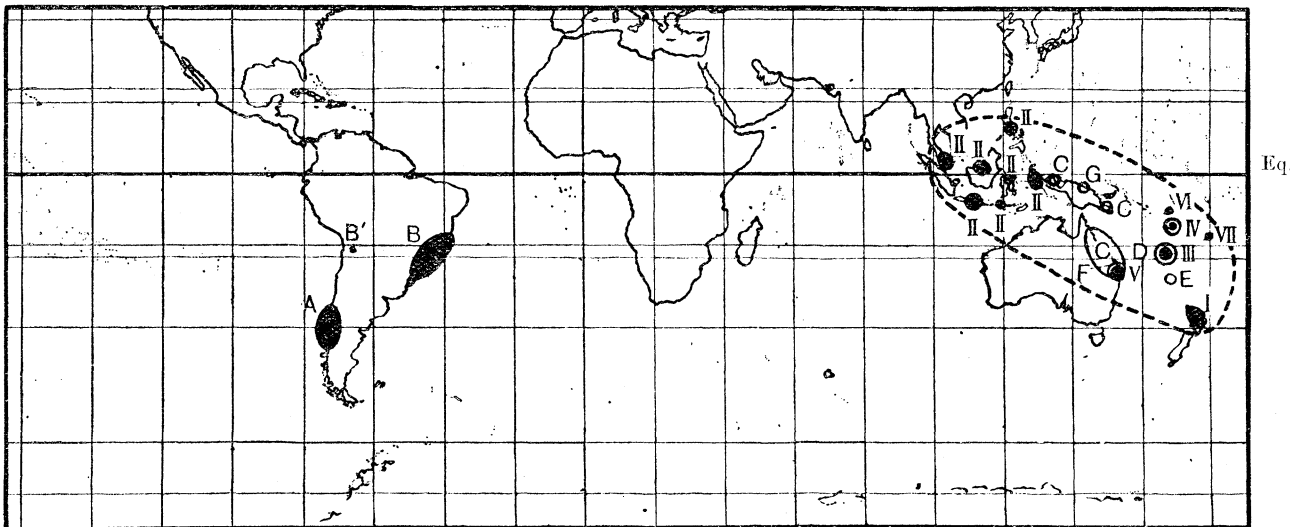
‡ DE JUSSIEU (1789), p. 413.

§ RICHARD (1826), p. 10.

Taxineæ, Cupressineæ, and Abietineæ, the members of the Abietineæ being *Pinus*, *Larix*, *Cunninghamia*, *Agathis*, and *Araucaria*. To these three groups DON\* added a fourth, the Araucarieæ, including *Araucaria*, *Dammara*, and "perhaps *Cunninghamia*." Twenty-six years later CARRIÈRE† restricted membership of the Araucarieæ to *Araucaria* and *Dammara*. In the *Genera Plantarum* HOOKER and BENTHAM‡ went a step further than DON, in definitely adding the genera *Cunninghamia* and *Sciadopitys*. Several later writers§ have adhered to DON's grouping of the three genera, *Araucaria*, *Dammara*, and *Cunninghamia*, under one family-name, but we follow EICHLER|| in excluding *Cunninghamia*. The numerous features shared by *Araucaria* and *Agathis* point to a close relationship, while the distinguishing features of *Cunninghamia* are amply sufficient to justify its omission from the Araucarieæ. We believe that *Araucaria* and *Agathis* are separated by a comparatively wide gap from other representatives of the Coniferales, and it is to these two genera, among recent Conifers, that our thesis is limited.

## II. DISTRIBUTION.

The accompanying map shows the approximate areas occupied by *Araucaria* and *Agathis* at the present day. The former distribution of this section of the



Map to illustrate the present Distribution of *Agathis* and *Araucaria*.

Gymnosperms is dealt with in section X, devoted to fossil forms, and as a convenient means of expressing the facts of distribution in a concise form we have made use of

\* DON (1841), p. 163.

† CARRIÈRE (1867), p. 593.

‡ HOOKER and BENTHAM (1880), vol. 3, pp. 423, 435.

§ BEISSNER (1891), MASTERS (1893), STRASBURGER (1872, 1879), VEITCH (1900).

|| EICHLER, in ENGLER and PRANTL (1889).



a form of map adopted by one of us in 1903.\* A few of the records of recent species are rendered of doubtful value through confused nomenclature, but we are chiefly concerned with the geographical extent of the family as a whole, rather than with the exact range of each specific type.

A. *Agathis*.—*Agathis* is scattered over an area extending from the Philippine Islands and the Malay Peninsula to the Kauri forests of New Zealand. *Agathis australis* (I) is said to extend from the North Cape of New Zealand to lat. 38° S., and the occurrence of sub-fossil trunks adds point to the statement that the forests are gradually dwindling.† *Agathis loranthifolia* (II) is mentioned by BECCARI‡ as occurring on the upper slopes of Mount Poe and on the plains of Kuching, in Borneo; it occurs also on the mountains of the Moluccas, in Java, Celebes, and the Sunda Islands, the Philippines and the Malay Peninsula. *Agathis robusta* (V) is scattered through the forest country near Wide Bay, in Queensland. *Agathis Moorei* (III) occurs with other members of the family in New Caledonia. *Agathis obtusa* (IV) is recorded from the New Hebrides. *Agathis macrophylla* (VI) was described by LINDLEY§ from the Queen Charlotte Islands, and SEEMAN|| is of opinion that this type may also be associated with *Agathis vitiensis* (VII) in the forest-flora of the Fiji Islands. From Mount Bartle Frere and the Mulgrave River, in Queensland, MUELLER¶ has recorded *Agathis Palmerstoni*.

With the exception of *Agathis robusta*, of Queensland, and the species from the Malay Peninsula, *Agathis* is essentially an island type. The genus is mentioned by RIDLEY\*\* with the ferns *Matonia* and *Dipteris* among the plants of Mount Ophir, in the Malay Peninsula,—three survivals from a remote past whose present range is but a feeble indication of their former abundance.

B. *Araucaria*.—With the exception of two well-defined species in South America, *Araucaria* is confined within the same area as that occupied by *Agathis*. *Araucaria brasiliensis*†† (B) flourishes at a height of 3000 feet in the forests of South Brazil and extends from lat. 29° 30' S. in Rio Grande do Sul northwards to San Paolo. PARLATORE‡‡ has described a form of this species from the mountains of Bolivia as *A. Saviana* (B'). The Chili pine, *Araucaria imbricata*,§§(A) occupies a zone 80 kiloms. broad and 250 kiloms. long, and, as in the case of *Agathis australis*, the occurrence of buried stems denotes a former extension of the Araucarian forests on the southern

\* SEWARD (1903), p. 3.

† KIRK (1889); HECTOR (1886), p. 98.

‡ BECCARI (1904), pp. 99, 100.

§ LINDLEY (1851), p. 271.

|| SEEMANN (1865), p. 264.

¶ MUELLER (1892), p. 45.

\*\* RIDLEY (1901), p. 7.

†† KARSTEN and SCHENCK (1903); NORTH (1892), p. 135.

‡‡ PARLATORE (1868), p. 369.

§§ HOOKER, W. J. (1835), p. 351; NEGER (1897).

slopes of the Andes. *Araucaria Rulci*\* (D) was first recorded from the summit of a lofty volcano on an island off New Caledonia, and it is said to occur also on the hills of Kanala, in New Caledonia.† The Bunya-Bunya, *Araucaria Bidwillii* (F), grows on the Brisbane range north-west of Moreton Bay, in Southern Queensland.

The most widely spread species of the Australian Araucarias is *A. Cunninghami* (C), which extends over an area 900 miles long in New South Wales and Queensland; this type is stated to occur also at an altitude of 6000 feet and upwards on Mount Obree, and at an altitude of 3000–4000 feet on Mount Arfak, in New Guinea.‡ The Norfolk Island pine, *Araucaria excelsa* (E), takes its name from the island where it was discovered by Captain COOK, and MUELLER records this species from New South Wales. *Araucaria Cookii* occurs in the New Caledonian Archipelago and in the New Hebrides. *Araucaria Balansæ* is recorded by BRONGNIART and GRIS§ from a height of 500 metres in New Caledonia, the home also of *A. Muelleri* and *A. Montana*.

One of the most remarkable facts as regards the distribution of *Araucaria* is the occurrence in New Caledonia of no less than five species of the genus.

### III. GENERIC DIAGNOSIS; NOTES ON SPECIES, ETC. i. *Agathis*.

The generic name *Dammara*, taken from Dammar-Puti, applied by islanders to the hard resin obtained from the tree, was first used by RUMPHIUS|| in a description of a plant from Amboyna, one of the Moluccas, which he named *Dammara alba*. In 1803 LAMBERT¶ figured and described as *Pinus Dammara* specimens of the same tree sent from Amboyna to Sir JOSEPH BANKS, and at a later date he adopted the name *Dammara orientalis*\*\*.

In 1807 SALISBURY†† proposed the name *Agathis* in place of *Dammara*. Both names are frequently used, but if we follow the rule of discarding pre-Linnean designations we must adopt *Agathis*.‡‡

In old trees, which may reach a height of 160 feet and a diameter of 12 feet, the trunk is usually bare for a considerable distance, forming a spreading head of branches at the summit. The branches are given off at approximately the same level, forming false whorls of four to six members, but their upward spring and the form of the leaves give to the trees a habit less formal than that of *Araucaria*.

\* SEBERT and PANCHER (1874), p. 168: 'Gard. Chron.' (1861), p. 868.

† PARLATORE (1868), p. 369.

‡ MUELLER (1887).

§ BRONGNIART and GRIS (1871), p. 206.

|| RUMPHIUS (1741), p. 174. Another plant described by RUMPHIUS as *Dammara selanica* is now referred to *Engelhardtia*, a Dicotyledon (RUMPHIUS, *loc. cit.*, p. 168, Plate 55).

¶ LAMBERT (1803), Plate 38.

\*\* LAMBERT (1824), p. 16.

†† SALISBURY (1807), p. 312; *ἀγαθίς* = a ball of thread.

‡‡ MUELLER (1892), p. 46.

The circular scars left on the fall of the branches constitute a notable feature in the stems of *Agathis*\* (Plate 23, c).

The leaves, which are usually sub-opposite, or opposite, on the lateral shoots, are arranged spirally on the main stem; they vary considerably in size, even within the limits of a species, ranging from 5 centims. long and 1 centim. wide in *Agathis australis* to 12 centims. long in *A. vitiensis*. They may be narrowly lanceolate, lanceolate-ovate, or elliptical in form. The leaves remain attached to the stem several years; in some cases stems apparently 10 years old retain functional leaves: they present a close external resemblance to those of certain species of *Podocarpus* (Sect.: NAGEIA),† but well-marked anatomical differences render the generic determination of detached leaves an easy matter.‡

The genus is dioecious, rarely monœcious. Male flowers solitary and axillary, having the form of cylindrical cones 2–3 centims. long and 1 centim. broad, with a few scale-leaves§ on the peduncle. The sporophylls, arranged in a close spiral, consist of a short horizontal stalk bearing several pollen-sacs and terminating in a triangular and vertical distal expansion. The microspores are without wings. Female flowers have the form of spherical (fig. 1, A) or broadly oblong cones, reaching

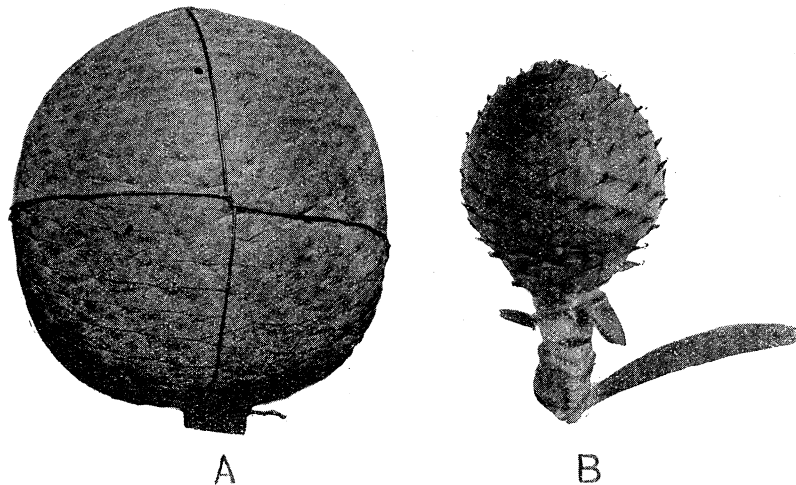


FIG. 1.—Female Flowers. A, *Agathis Moorei* ( $\frac{1}{2}$  nat. size); B, *A. australis* ( $\frac{3}{4}$  nat. size).

in some cases a length of more than 10 centims. Cone-scales, in spiral sequence with the leaves, are broadly triangular with the wide distal margin bent at right-angles to the rest of the scale. The cone of *Agathis australis*, represented in fig. 1, B, shows a gradual transition from foliage leaves to sporophylls. The scales are attached by a narrow proximal end to the stout cone-axis from which they fall on the ripening

\* See p. 312.

† ENGLER and PILGER (1903), pp. 58 *et seq.*

‡ See p. 317.

§ LAMBERT (1828), Plate 6.

of the seeds. Each fertile scale bears a single seed with one or rarely two wings (fig. 24, A—D, p. 359). The embryo has two cotyledons.\*

a. *Some Points in the Gross Anatomy of the Stem of Agathis.*

The young stem of *Agathis* (e.g., *A. robusta*) is covered with spirally disposed leaves: the free laminæ have been removed from the twig shown in Plate 23, fig. 2, A, in order to expose the decurrent leaf-bases; the position of a former terminal bud is shown by the more crowded leaf-bases. The leaves persist for a considerable time after the formation of cork, and their stretched bases form narrow ridges (fig. 2, B). The method of disarticulation of the branches was described by SHATTOCK† in 1888. As shown in the photograph of a stem of *A. robusta*, reproduced in fig. 2, C, the clearly defined branch-scars bear a resemblance to the large oval or circular depressions which characterise the *Lepidodendroid* stem known as *Ulodendron*; SHATTOCK drew attention to the similarity of the scars, but decided that their method of formation in the recent genus does not afford a clue to the nature of those of *Ulodendron*. The generally accepted explanation of the scars in the Palæozoic stems—namely, that they have been produced by the pressure of the bases of cones against the surface of the growing stem—does not seem to us entirely satisfactory.

The method of attachment of the lateral branches to the stem presents some features of interest from the point of view of plant-architecture. If a stem, such as that shown in fig. 2, B, be cut across longitudinally through the centre of the branch and the base of a subtending leaf, it becomes at once apparent that the branches do not arise approximately at right-angles to the stem as one would have expected from the external relations of branch and stem; the woody cylinder of the branch, as seen in fig. 3, A, passes in a steeply descending direction until it becomes incorporated with the wood of the stem. The broad pith of the branch is slightly expanded at the region of junction between the cortex of branch and stem, and then it gradually decreases in diameter until it becomes continuous with the pith of the stem. The cortex of the stem above the insertion of the branch passes down as a narrow extension between the wood of stem and branch, and eventually joins the pith of the main axis (fig. 3, A and C).

This relation between the stem and secondary branches is in marked contrast to that in *Araucaria*, in which the wood of the branch, is given off almost at right angles from that of the trunk. The sharp bend of the wood of a branch of *Agathis* (fig. 3), as it passes within the stem-cortex, probably has the effect of giving a greater flexibility to the lateral branches. Another structural feature connected with branch-insertions is illustrated by the two diagrammatic sketches reproduced

\* KIRK (1889), Plate 80A.

† SHATTOCK (1888).

in figs. 3, B and C. The transverse section, fig. 3, B, shows the wood and cortex of a stem 5 centims. in diameter, with the woody cylinders of two branches *b* and *b'*. The branch *b* is separated from the wood of the stem by a patch of cortical tissue (*cf.* fig. 3, A). Fig. 3, C, which represents a section from a considerably lower level, shows the branch *b* enclosed between the two prominent cheeks of the stem-wood and with the two piths in continuity.

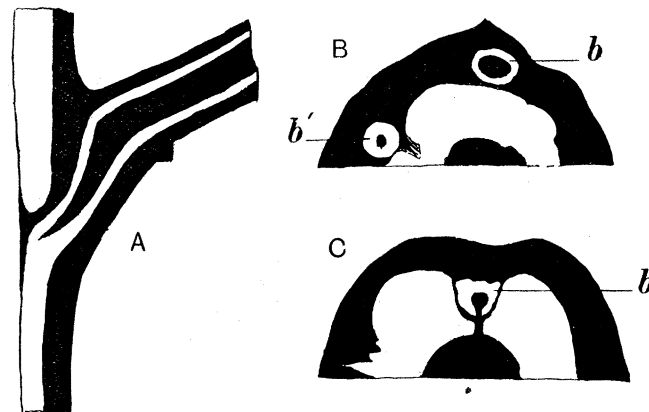


FIG. 3.—*Agathis robusta*. Diagrams illustrating the attachment of Lateral Branches.  
(The wood is unshaded.)

#### b. *List of Species.*

Broadly speaking, *Agathis australis* constitutes one clearly defined type, while the other species exhibit a close agreement as regards both leaf-form and reproductive shoots. It is by no means improbable that a more thorough examination of some of the forms may lead to a slight reduction in the number of well-marked species.

*Agathis australis* (Kauri Pine). Figs. 1, B; 4, A, B.

1824. *Dammara australis*,\* LAMBERT, Pinus, p. 15.

This species, (introduced into Europe 1823), is described by HECTOR† as the finest forest tree of New Zealand, its stems rising “like massive columns” to a height of 160 feet.

*Leaves.*—The sessile leaves are smaller than those of other species, and are characterised also by a thicker and more leathery lamina. On young shoots the leaf lamina is thin and narrow, reaching a length of more than 7 centims. with a breadth of about 1 centim. (fig. 4, A); on older shoots the average length of the leaves is between 4 and 5 centims., and 1 centim. broad; occasionally a leaf occurs of a broader and more oval form (2·5 centims. long and 1·4 centims. broad (fig. 4, B). The narrow lanceolate lamina is traversed by about 15 veins, usually bifurcating

\* For drawings of this species see LAMBERT (1824); ‘Flore des Serres,’ vol. 11 (1856); ‘Gard. Chron.,’ vol. 20 (1883), p. 515; KIRK (1889).

† HECTOR (1886).

near the base. The terminal buds are enclosed by short and broad scale-leaves, the lower of which, with longer laminæ, are almost identical with the foliage leaves.

*Cones*.—Male flowers between 3 and 4 centims. long, terminating in a blunt apex and rather more than 1 centim. broad. Each sporophyll—5·5 millims. long—bears 10–12 pollen-sacs. The female cones (fig. 1, B) terminal on short lateral branches, are approximately globose, 6 centims. long and 6 centims. broad, distinguished by their smaller size from those of other species.

*Agathis loranthifolia* (Amboyna Pitch-tree). Fig. 24 E.

1741. *Dammara alba*,\* RUMPHIUS, "Herb. Amboin," Part II, p. 174, Plate 42.

A species (introduced 1804) fairly widely scattered over the Malayan-Polynesian region.

BECCARI† refers to the occurrence of *Agathis Beccarii* Warb. on the upper slopes of Mount Poe, and of *A. Borneensis* Warb., in the forests of the plain near Kuching, in Borneo. He regards both these as varieties of *Dammara alba*.

The shortly-stalked leaves are more typical of the genus than are the smaller ones of the Kauri pine; the lamina of exceptionally large leaves may reach a length of 13 centims., and a breadth of 5 centims. They vary in form from broadly lanceolate to ovate; the apex may be blunt, but it is sometimes sufficiently acuminate to assume the appearance of a short drip-tip.

The male flowers are similar to those of *A. australis*: the pollen-sacs are said to vary in number from 8 to 18.‡ The female cones, which may attain a diameter of 10 centims., are of the usual globose type.

*Agathis robusta* (Australian Kauri). Plate 23, Figs. 2, 3; Plate 24, Fig. 21, c.

1860. *Dammara robusta*, MUELLER, 'Trans. Pharm. Soc.,' Victoria, II, p. 174.

This Queensland species presents a close resemblance to *A. loranthifolia*, especially as regards the shape of the shortly stalked leaves of which the lamina is 5–6 centims. broad, terminating in an acuminate apex, and reaching a length of 15 centims.

The sporophylls of the male flowers are described by THIBOUT§ as having only three pollen-sacs. The female cones (10–12 centims. long and 6–8 broad) are rather less globular than those of the preceding species.

\* For illustrations see RUMPHIUS (1741), LAMBERT (1803), SALISBURY (1807), RICHARD (1826); GRIFFITH (1854); 'Bot. Mag.' (1883), Tab. 5359.

† BECCARI (1904), p. 100.

‡ RICHARD (1826), p. xix.

§ THIBOUT (1896), p. 109, Plate 10, fig. 18.

*Agathis Moorei*. Figs. 1, A ; 4, C, D ; 24, A-D.

*Dammara Moorei*, LINDLEY, 'Journ. Hort. Soc.,' vol. 6, 1858, p. 271.

The leaves of this New Caledonian type vary considerably in size and shape ; some, especially the leaves of young shoots, are comparatively long and narrow (fig. 4, c) (13 centims.  $\times$  2 centims.), others have a lamina 6 centims. in length and 1.2 centims. broad ; occasionally the leaves assume a much broader and more oval outline (13 centims.  $\times$  4 centims.) with an obtuse apex (fig. 4, d).

The cones (fig. 1, A) exhibit features similar to those of other species. A specimen of a female cone in the Kew Museum has a length of 14 centims., and a breadth of 11 centims.

*Agathis obtusa*.

1858. *Dammara obtusa*, LINDLEY, 'Journ. Hort. Soc.,' vol. 6, p. 270.

The leaves of this species, discovered by Mr. MOORE in the New Hebrides,\* are stiffer and more like those of *A. australis*, with a blunt apex and crowded veins, the lamina reaching a length of 12 centims. and nearly 3 centims. broad. The cones are of similar form to those of *A. loranthifolia* and *A. robusta*.

*Agathis macrophylla*. Fig. 4, E.

1851. *Dammara macrophylla*,† LINDLEY, 'Journ. Hort. Soc.,' vol. 6, p. 271.

The leaves of this tree, a native of one of the Queen Charlotte Group of Islands, are described by LINDLEY as large, ovate, lanceolate, and acute, having a length of 17 centims. and a breadth of 5 centims. A specimen in the Kew Herbarium (shown in fig. 4, E) labelled "*Podocarpus*, New Hebrides, LINDLEY, 1852," no doubt belongs to this species.

The cones conform to the usual type, measuring approximately 11 centims. by 9 centims. ; the cone-scales are larger than those of *A. robusta*.

*Agathis vitiensis*. Figs. 4, F ; 24 F.

1865. *Dammara vitiensis*, SEEMAN, 'Flor. Vit.,' p. 265, Plate 76.

This species is described by SEEMAN as growing as an isolated tree in the forests of Fiji. The leaves (fig. 4, F), which are very similar in form to those of *A. loranthifolia* and *A. robusta*, may reach a length of 15 centims. and a breadth of 4.5 centims., but as a rule the leaf is narrower than in *A. robusta*.

\* LINDLEY (1851), p. 270.

† For illustration see HOOKER, W. J. (1852).

*Agathis Palmerstoni.*

1892. *Dammara Palmerstoni*, MUELLER, 'Vict. Naturalist,' vol. 8, p. 45.

MUELLER described this species from Mount Bartle Frere and the Mulgrave River (Queensland), regarding it as nearest to the New Caledonian species *A. Moorei*. The leaves are comparatively small, narrow, elliptical and bluntly terminated.

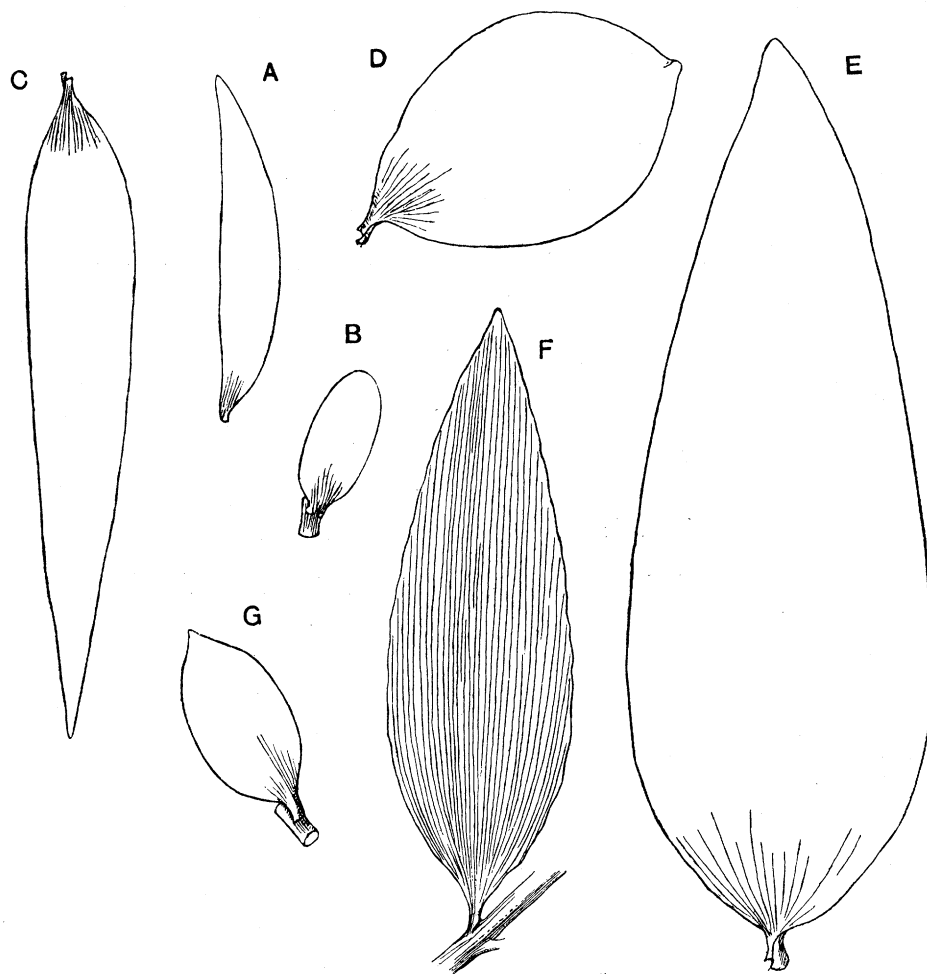


FIG. 4.—A—F, Leaves of *Agathis*; A, B, *A. australis*; C, D, *A. Moorei*; E, *A. macrophylla*; F, *A. vitiensis*; G, *Podocarpus*, sp.

c. DOUBTFUL SPECIES.

*Agathis hypoleuca*.—HENKEL and HOCHSTETTER\* speak of "*Dammara hypoleuca* MOORE" from New Caledonia, as apparently distinct from all known species. The young trees are described as having long lanceolate leaves; the older form is unknown. In all probability this plant is identical with *A. Moorei*.

\* HENKEL and HOCHSTETTER (1865).



*Agathis Veitchii*.—The same authors\* instituted the name *Dammara Veitchii* from a young plant obtained from seeds brought to England from Japan by Mr. JOHN VEITCH. In all probability this plant was a species of *Podocarpus*, a genus represented in the Japan flora by members of the section *Nageia*.

## SPECIES INCORRECTLY REFERRED TO AGATHIS.

The name *Dammara Motleyi* occurs in a list of plants published by PARLATORE† with a short diagnosis. In a paper on *Podocarpus vitiensis*, SEEMANN‡ gave a brief description of *Dammara Motleyi* founded on a vegetative shoot obtained from near Bangarmassing in Borneo. The leaves are described as 3–4 centims. long, 15–21 millims. broad, shortly stalked, opposite and oval (fig. 4, g). SEEMANN recognised the possibility that the Bornean plant might be a *Podocarpus*, a genus with which a sterile shoot of *Agathis* might be easily confounded.

The examination of a leaf from a vegetative twig in the Kew Herbarium collected by J. MOTLEY from Bangarmassing shows that SEEMAN was correct in his surmise that PARLATORE's species might be a *Podocarpus*. The lamina, which is almost isobilateral, is characterised by the occurrence of resin-canals between the vascular bundles, and by numerous thick-walled fibres, with hardly any lumen, below the epidermis. In this and other features the anatomy conforms to that of the leaves of *Podocarpus Nageia*.

GENERIC DIAGNOSIS, ETC. ii. *Araucaria*.

The generic name *Araucaria* was first used by DE JUSSIEU§ in 1789 for a plant originally described by Molina|| as the most beautiful of the trees of Chili, and named by him *Pinus araucana*. To the same plant LAMARCK¶ gave the name *Dombeya chilensis*.

In 1807 SALISBURY\*\* proposed the name *Eutassa*†† for the Norfolk Island pine (*Araucaria excelsa*); the Chilian pine (*A. imbricata*) he designated *Columbea*‡‡. In 1847 ENDLICHER§§ made use of SALISBURY's term *Columbea* as a sectional or subgeneric title, and for *Eutassa* he substituted the subgeneric designation *Eutacta*. The Section COLYMBEA comprises *Araucaria imbricata*, *A. brasiliensis*, *A. Bidwillii*,

\* HENKEL and HOCHSTETTER (1865), p. 217.

† PARLATORE (1862), p. 26.

‡ SEEMANN (1863).

§ JUSSIEU (1789), p. 413.

|| MOLINA (1786), p. 157; (1809) p. 150.

¶ LAMARCK (1786), p. 301, Plate 828.

\*\* SALISBURY (1807), p. 316.

†† “*εὖ* = bene, *τάσσω* = ordino: nomen a ramis foliisque quasi artificiose collocatis” (SALISBURY, p. 317).

‡‡ “*κολυμβάω* = nato: ob materiam navium malis peridoneam”

§§ ENDLICHER (1847), p. 186.

species characterised by flat leaves, wingless cone-scales, hypogean germination, also by their relatively larger cones and by verticillate stamens. Under EUTACTA are grouped *A. excelsa*, *A. Cookii*, *A. Cunninghamii*, *A. Balansa*, *A. Rulei*,\* *A. Muelleri*, forms in which the leaves of the adult plants are more needle-like and keeled, the cone-scales possess thin winged margins and the germination is epigean, the cone relatively smaller, and the stamens in spirals.†

Older trees of *Araucaria*, like those of *Agathis*, are usually characterised by tall columnar stems reaching a height of 200 feet, bare of branches for the greater part of their length, and forming a candelabra-like head consisting of spreading horizontal shoots terminating in tufts of smaller branches.‡ The branches arise in false whorls, 4–15 in each “whorl.”

The relatively large and flat leaves are arranged in dense spirals; the lamina is broad and coriaceous, and traversed by several veins (Sect.: COLYMBEA), or the leaves may be linear, subulate, falcate, four-angled, more or less laterally compressed, and traversed by one or occasionally by more than one vein (Sect.: EUTACTA). The leaves of fertile and sterile shoots of the same species frequently differ in size and shape. In some species the leaves remain on the tree for 10 or even 15 years.

The buds are devoid of true bud-scales; the smaller foliage-leaves which have served for bud-protection are shown on the branches of *Araucaria Bidwillii*, where they occur at intervals as leaves of reduced size (fig. 5).

*Araucaria* is dioecious, but in rare instances both male and female cones have been produced on the same trees.§ The male flowers (figs. 8, B; 10; 11, C F; 13, A), which are either solitary or clustered (terminal in Sect.: EUTACTA; axillary in Sect.: COLYMBEA), may reach a length of 25 centims. (*A. Bidwillii*, fig. 8, B), or a breadth of 3–4 centims. (e.g., *A. Muelleri*, fig. 11, D). The sporophylls, like those of *Agathis*, consist of a horizontal pedicel terminating in a distal expansion prolonged in some species into a gradually tapering vertical lamina (figs. 11, E; 22, B); the pollen-sacs (6–20) are arranged in two series and lie parallel to the pedicel, their proximal ends being attached to the distal expansion of the sporophyll.

The female cones, which reach maturity in two, or sometimes in three, years (fig. 12) are oval or globose, the larger ones attaining a diameter of 20 centims. They consist of a stout central axis|| bearing crowded, spirally-disposed, deciduous cone-scales (fig. 8, A, C). The cone-scales constitute a continuous series with the

\* The species *A. Rulei* is placed by PARLATORE under the section Colymbea, but it would seem to be more correctly included with the Eutacta species.

† THIBOUT (1896), p. 106. THIBOUT's statement is based on facts obtained from such species as he examined.

‡ KARSTEN and SCHENCK (1903).

§ ‘Gard. Chron.’ (1890), p. 587; PARLATORE (1861), p. 85.

|| MARTIUS (1852), Plate 90; ‘Gard. Chron.’ (1861), p. 868.

foliage-leaves. Each fertile scale in Sect.: COLYMBEA consists of a deep and comparatively narrow ovuliferous scale enclosing a single ovule. In Sect.: EUTACTA the scale is much broader and flatter, the edges forming thin membranous wings which take the place of the seed-wing in *Agathis*.

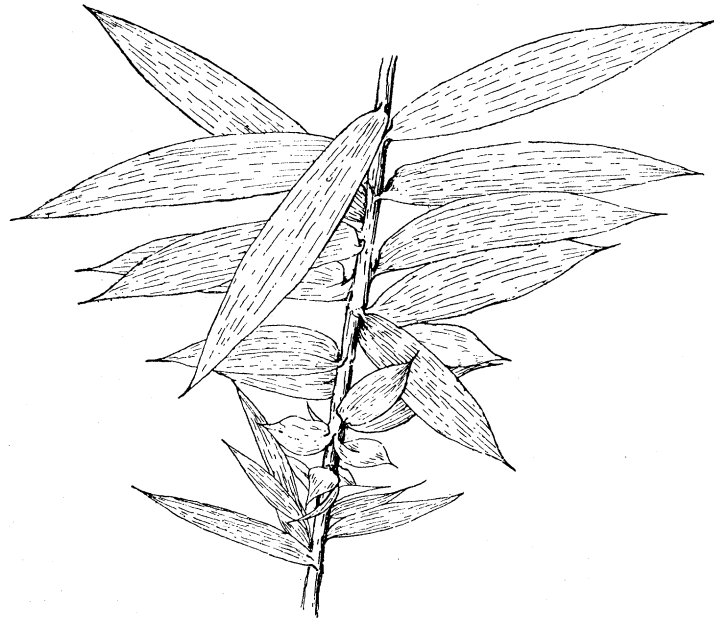


FIG. 5.—*Araucaria Bidwillii* (nat. size).

The cone-scales of all species of *Araucaria* are characterised by a more or less prominent outgrowth from the upper surface, between the base of the ovule and the distal end of the scale. In some species (e.g., *A. Bidwillii*, fig. 24, L, M, l) this outgrowth, the so-called ligule, forms a conspicuous feature, while on others it is reduced to a spinous projection (e.g., *A. Cookii*, fig. 24, G, l).\*

The seedlings in Sect.: EUTACTA have two to four epigeal cotyledons (figs. 14, B; 15); in Sect.: COLYMBEA two hypogean cotyledons are present (fig. 28, O, P), and a more or less tuberous hypocotyl (fig. 13, B—D) which serves as a food-store.

a. *Some Points in the External Features of an Araucarian stem, illustrated by A. imbricata.*

The different forms assumed by the external surface of the main stem of *A. imbricata* at different stages of growth have been briefly described by BALFOUR in his 'Palæontological Botany' † as affording an object-lesson for the benefit of botanists or geologists engaged in the identification of fossil stems. It is well known that the various appearances presented by the surface of certain stems

\* For figures and further description of cone-scales see p. 359, fig. 24.

† BALFOUR (1872), p. 5. figs. 2—6.

consequent on the increase in girth and on the development of cork have been responsible for the institution of several unnecessary generic names. The surface of a young stem of *A. imbricata* (Plate 23, fig. 6) entirely covered with prominent leaf-bases,\* suggests a comparison with the leaf-cushions of *Lepidodendron*. The ridges seen on the cushions in fig. 6, A, are the result of contraction of the tissues on drying. Fig. 6, B represents a later stage (several leaves have been removed) in which the laminæ are still fresh, but the cushions have assumed a different form due to the growth of the stem. This stage recalls the surface-characters of some species of *Sigillaria*. The next stage (fig. 6, C) shows the leaves still almost intact, but the superficial tissues of the cushions exhibit signs of wrinkling and splitting. This is succeeded by the condition shown in fig. 6, D, in which the laminæ have fallen off, but here and there torn remnants are still visible; the radiating lines of splitting are more prominent than in fig. 6, C. A still older stem (fig. 6, E) is characterised by more tangentially elongated ridges marking the positions of leaf-attachments; the cushions, which still preserve their individuality, are furrowed by numerous cracks, which are indistinctly shown in the reduced photograph.

An old tree from Kew† showed several interesting features. The wood with well-marked rings of growth was covered with a loosely-adherent dry bark, composed on its inner side of a feltwork of fibres. The inner face of the bark, after removal of the fibres, is represented in fig. 6, G; the points of exit of the leaf-traces are seen as small circular pits. This surface-appearance is of interest as bearing some resemblance to certain fossil stems from the Lower Greensand of Kent, originally referred by KÖNIG to *Dracena*, and more recently named *Benstedtia*‡ and compared with stems of the recent genus *Zamia*. A French author§ who has described similar fossil stems compares them with *Araucaria*.

The external surface of the bark, of which the inner face is shown in fig. 6, G, is represented in fig. 6, F. The leaf-areas are no longer preserved, and the bark has begun to split by oblique longitudinal fissures, a preliminary stage in the process of splitting which ultimately produces the curious appearance characteristic of old trunks as seen in the Chilian Andes. Even on the older parts of the Kew tree, especially below the insertion of the branches, portions of split and torn laminæ of leaves are still retained.

The comparatively large diameter of the pith is a characteristic feature of both *Araucaria* and *Agathis*. In a stem of the former genus with wood 20 centims. in diameter the pith was found to vary in breadth from 1 centim. to more than 2 centims.||

\* The laminæ have been cut off in order to expose the leaf-bases.

† See page 321.

‡ SEWARD (1895), p. 169; for drawings see SEWARD (1896).

§ FLICHE (1900<sup>2</sup>); SEWARD (1903<sup>2</sup>), p. 35.

|| See POTONIE (1899), p. 295, for figures of pith-casts of *Araucaria*, exhibiting characteristic periodic swellings.

b. *List of Species.*

Sect. : COLYMBEA. *Araucaria imbricata* (Chile Pine). Plate 23, fig. 6 ; figs. 7 ; 13, c, D ; 16 ; Plate 24, fig. 17 ; fig. 18 ; Plate 24, fig. 21, A, B, D ; figs. 23 ; 24, K ; 25, D ; 26, B ; 27 ; 28.

1786. *Dombeya chilensis*,\* LAMARCK, 'Ency. Méth.,' II, p. 301, Plate 828.

1797. *Araucaria imbricata*, PAVON, 'Mem. Real. Acad. Med., Madrid,' † v. i, p. 199.

*Araucaria imbricata*.—An interesting account has been published in the 'Kew Bulletin' ‡ of the introduction into England of this species in 1796. ARCHIBALD MENZIES, a naval surgeon who accompanied Captain VANCOUVER in his Survey voyage (1791–95), was the means of introducing the tree in the following circumstances. At a dinner given by the Viceroy of Chile to the officers of the ship, some nuts formed part of the dessert ; MENZIES took a few on board with him and planted them in a box of earth, with the result that five plants of *A. imbricata* were brought to England. According to LOUDON, MENZIES presented the young trees to Sir JOSEPH BANKS, who sent some to Kew. MASTERS,§ in 1892, referred to a tree still growing at Kew as the only survivor of the original batch. In 1894 the Kew tree was cut down, and portions of the trunk were subsequently handed over to one of us by Sir WILLIAM THISELTON-DYER.

PAVON|| was the first writer to refer the Chilean Pine to the genus *Araucaria* in preference to LAMARCK's genus *Dombeya* under the specific name *imbricata*. *A. imbricata*, formerly spoken of as Sir JOSEPH BANK'S Pine, is now one of the most familiar conifers in cultivation ; it is said to flourish in the Island of Shapinstay, one of the Orkneys,¶ and HANSEN speaks of it as growing as far north as Molde (62° 44') and Balestrand (60° 15'), in Norway.\*\*

The habit of the "Monkey Puzzle," as seen in a well-grown British tree, is that of a pyramid with the lowest branches almost devoid of lateral shoots and bending down to trail like prickly snakes on the grass (fig. 7).†† In the Chilean Andes‡‡

\* For illustrations see LAMBERT (1824 and 1820) ; RICHARD (1826) ; FORBES (1839) ; 'Flore des Serres,' vol. 15, Tab. 1557–80 ; 'Gard. Chron.' (1872), p. 1324 ; 'The Garden,' Jan. 22, 1876 : '*Pinetum Brit.*' (RAVENSCROFT), vol. 1, 1884 ; 'Gard. Chron.' (1890), pp. 587, 593 ; NEGER (1897) ; Miss NORTH'S Pictures (Kew), Nos. 4 and 6.

† This work is to be found in the library of the Royal College of Surgeons, London.

‡ 'Kew Bulletin' (1891), p. 299 ; (1893), p. 24.

§ MASTERS (1892), p. 14.

|| PAVON (1797).

¶ MASTERS (1892), p. 87.

\*\* HANSEN (1892), p. 342.

†† We are enabled, through the kindness of the EARL OF ANNESLEY, to reproduce this photograph, which he took for us in the Castlewellan Gardens, county Down.

‡‡ NEGER (1897). The habit of young and old trees is clearly shown in a photograph presented by Mr. ELWES to the Kew Herbarium of several trees in the Lolco Valley, at an altitude of 4000 feet.

the younger trees exhibit the familiar pyramidal form, but in the older ones the trunk is bare for about three-fifths of its length, and terminates in a candelabra-like head which gives them a certain resemblance to the characteristic form of the Stone Pine (*Pinus Pinea*).



FIG. 7.—*Araucaria imbricata*, in the EARL OF ANNESLEY'S Garden, Castlewellan, co. Down.

The branches, often in regular "whorls" of five, are covered with thick lanceolate leaves terminating in a sharp point and traversed by several parallel veins.

The male flowers are borne in clusters, reaching a length of 8 centims. and 5 centims. in diameter. The sporophylls are characterised by the comparatively long, upturned, distal lamina bearing 16–20 pollen-sacs (fig. 23). The female cones are more or less globose, and may be 15 centims. long. The cone-scales completely enclose the ovules. The seedlings of this species, like those of *A. Bidwillii*, differ from the young plants of the species of Sect. : EUTACTA in having a swollen hypocotyl and two hypogean cotyledons (fig. 13, c, d).

*Araucaria brasiliensis*. Figs. 8, A; 20, E; 24, N, O.

1820. *Colymbea angustifolia*, BERTOLONI,\* 'Piant. Brasile,' p. 7.

1822. *Araucaria brasiliensis*, RICHARD, 'Dict. Class. d'hist. nat.' I, p. 512.

This Brazilian species (introduced 1819) was originally recognised by RICHARD† as a distinct type. The habit of old trees is well shown in a recently published photograph of a forest of *A. brasiliensis* growing on the Hochland of the Parana State.‡ The bare trunks terminate in an umbrella-like crown of wide-stretching branches, 4–8 in each "whorl." Most of the tertiary branches are thrown off so that the tips of the main branches form dense tufts. Miss NORTH describes the tree as having three distinct stages and characters of form; in the first "it looks like a perfect cone; in the second a barrel with a flat top getting always flatter as the lower branches drop off, till in its last stage none but those turning up are left, and it looks at a distance like a stick with a saucer balanced on the top."§

The habit of this species is more lax and spreading than in the other members of the genus.

The loose spreading and glaucous leaves are a characteristic feature of the species; they are narrower and less stiff than those of *A. imbricata*. The narrow lamina may reach a length of 6–7 centims.; on the fertile branches the leaves are shorter and broader. The male flowers may be 10–13 centims. long.

The female cones are globose (fig. 8, A), and may reach a diameter of 20 centims. The swollen distal ends of the scales are characterised by a circular umbo (fig. 24, N, O), and bear a resemblance to those of *Pinus Pinaster*. A figure given by MARTIUS|| shows the thick cone-axis, a characteristic feature of the genus.

*Araucaria Bidwillii* (Bunya Bunya). Figs. 5; 8, B; 13, B; 19; 24, L, M.

1843. *Araucaria Bidwillii*, HOOKER, 'London Journ. Bot.,' p. 498, Plates 18, 19.

1847. " " ANTOINE,¶ 'Conif.,' p. 106, Plates 46–7.

This species was obtained by Mr. BIDWELL in South Queensland, and brought to England in 1843.\*\* It is said to attain a height of 150 feet and produces 10–15 branches in each "whorl."

\* For illustrations see LAMBERT (1824, 1828), FORBES (39), ANTOINE (1840), ZUCCARINI (1840), MARTIUS (1852), SIEBOLD (1870); 'Flore de Serres' (1875), Tab. 2202; 'Gartenflora' (1887), p. 197; 'Gard. Chron.' (1888), p. 774; KARSTEN and SCHENCK (1903).

† RICHARD (1822), p. 512.

‡ KARSTEN and SCHENCK (1903), Plate 6; see also 'Gard. Chron.' (1888), p. 775, fig. 105. The reproduction from Martius in Engler and Prantl does not represent the typical habit of the species.

§ NORTH (1892), p. 135.

|| MARTIUS (1852), Plate 110.

¶ ANTOINE's work bears the date 1846–47 (112 pp., 53 plates). It is probable that the part including *A. Bidwillii* was published a year or two earlier than 1847.

\*\* HOOKER, W. J. (1843), p. 502, Plates 18, 19.

The acute, sessile leaves (fig. 5) have the flat form characteristic of the section *Colymbea*, but are narrower and less stiff than those of *A. imbricata*; the longer ones have a lamina more than 7 centims. long and are practically identical with those of *A. Hunsteinii* (fig. 9). The leaves on the main stem are comparatively short and broad, while those on the lateral branches are longer.

*Cones*.—The male flowers (fig. 8, B) attain a length of 20 centims. and a breadth of 1.5 centim.

The female cones, which are the largest in the genus, come to maturity in three years. A specimen in the Kew Museum measures approximately 28 centims. in diameter. The scales (fig. 24, L, M) are broader and thicker than in *A. imbricata* and produce oval seeds, with two slightly prominent keels, reaching a length of 5 centims. and a breadth at the base of 2–3 centims.

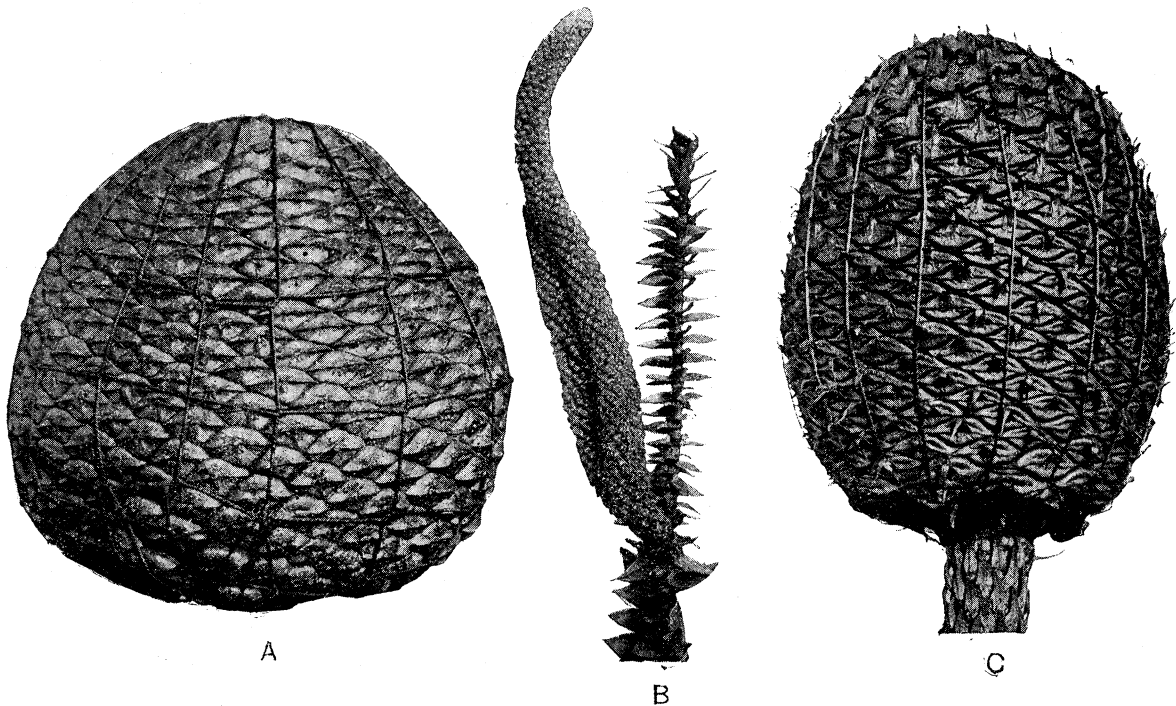


FIG. 8.—A, female flowers of *Araucaria brasiliensis*; B, Male flower of *A. Bidwillii*; C, Female flower of *A. Cunninghamii*.

(A,  $\frac{4}{9}$  nat. size; B,  $\frac{10}{27}$  nat. size; C,  $\frac{16}{21}$  nat. size.)

*Araucaria Hunsteinii*. Fig. 9.

1889. *Araucaria Hunsteinii*, SCHUMANN and HOLBURG, 'Flor. Kais. Wilh. Land.,' p. 11.

This species, described by SCHUMANN,\* from an altitude of 1300 metres in Kaiser Wilhelms Land, bears a close resemblance in its vegetative shoots to *A. Bidwillii*.

\* SCHUMANN (1889).



SCHUMANN recognises the similarity, but considers that in the size and texture of the leaves as well as in the form of the male sporophylls *A. Hunsteinii* is worthy of specific recognition.

*Leaves.*—Linear-lanceolate or ovate-lanceolate, 5–10 centims. long and 1–1·2 centim. broad.

*Cones.*—Male flowers 20 centims. long and 2·5 centims. broad, having an appearance “almost Lycopodium-like.”

Female cones 6 centims. long and 7·5 in diameter.

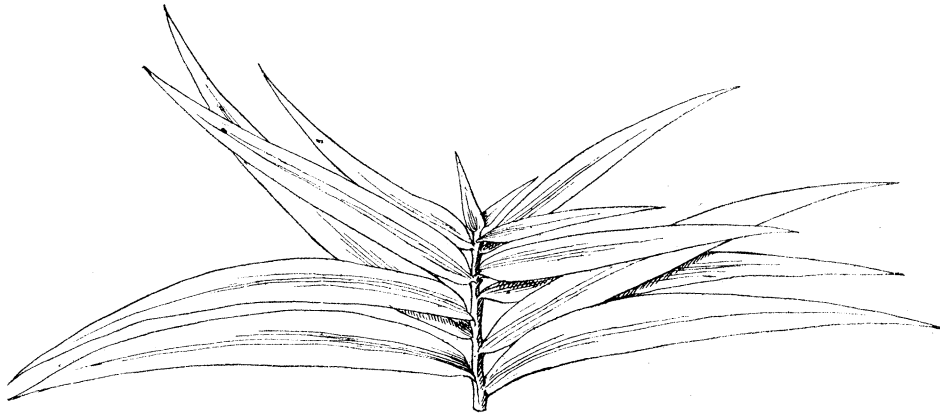


FIG. 9.—*Araucaria Hunsteinii* ( $\frac{2}{3}$  nat. size).

Sect. : EUTACTA. *Araucaria Cunninghamii* (Moreton Bay Pine). Fig. 8, c.

1839. *Araucaria Cunninghamii*, FORBES,\* ‘Pinet. Woburn.,’ Plate 52.

*A. Cunninghamii* (introduced 1827) is the most widely spread of the Australian species; it presents a close resemblance to *A. excelsa* and *A. Cookii*. During Captain COOK’s first voyage SIR JOSEPH BANKS and Dr. SOLANDER saw a tree on the East Coast of New Holland which they supposed to be identical with the Norfolk Island pine, but ALLAN CUNNINGHAM, who sent some plants to Kew, recognised points of difference from *A. excelsa*.†

The falcate and sharply pointed leaves are of the same type as those of *A. excelsa* and *A. Cookii*. The difference between the young and old foliage is illustrated by BAUER’s drawings in ANTOINE’s work.‡

*Cones.*—Male flowers 5–8 centims. long. Female cones 7–8 centims. long (fig. 8, c) similar to those of *A. excelsa*.

\* For illustrations see FORBES (1839), ANTOINE (1847), SIEBOLD (1870), ‘Gard. Chron.’ (1888), p. 684; ‘Gartenflora’ (1888), p. 865.

† HOOKER, W. J. (1843).

‡ ANTOINE (1840), Plates 43, 44; SIEBOLD (1870), Plate 139.

*Araucaria excelsa* (Norfolk Island Pine). Figs. 10; 14; 24, H, I.

1786. *Cupressus columnaris*, FORSTER,\* 'Prod. Prod. Ins. Austrl.,' p. 67.

1803. *Dombeya excelsa*, LAMBERT, 'Pinus,' Plates 39-40.

This species was introduced to Kew by Sir JOSEPH BANKS in 1793. The Norfolk Island Pine was discovered by Captain COOK, who spoke of the stems as resembling basaltic columns; but, he adds, on nearing the island "everyone was satisfied that they were trees, except our philosophers, who still maintained they were basaltes."† LAMBERT speaks of a tree on Norfolk Island measured by Governor KING having a length of 228 feet and a girth of 11 feet.‡ The leaves are either spreading and falcate, laterally compressed (10-15 millims. long) or shorter and relatively broader and imbricate; this difference in the leaves is shown in BAUER's drawings published by ANTOINE.§



FIG. 10.—*Araucaria excelsa*, male flower.  
(Nat. size.)

The female cones, of more or less spherical form, are rather larger than those of *A. Cookii* and *A. Cunninghamii*, but the cone-scales are of the same general type in all three species. An abnormal cone of this species borne on a tree in Madeira is described in the 'Gardeners' Chronicle' for 1881,|| in which the scales are said to be seedless and wingless.

Male flowers oblong, 4 centims. long (fig. 10); the sporophylls having 10-12 pollen-sacs.

*Araucaria Cookii*.¶ Figs. 11, A-C; 12; 15; 24, G.

1841. *Araucaria Cookii*, R. BROWN (DON), 'Trans. Linn. Soc.,' vol. 18, p. 164.

This species, discovered in 1774 during Captain COOK's second voyage,\*\* and named by ROBERT BROWN,†† is said to be characterised by a columnar form due to the production of short branches in place of the longer deciduous shoots, which project almost at right angles to the trunk, rising vertically to a height of 200 feet, and terminating in a pyramidal apex.

\* For illustrations see 'Flore de Serres' (1877), vol. 21, Tab. 2304-5; FORBES (1839), ANTOINE (1847); SIEBOLD (1870).

† HOOKER, W. J. (1852); HOOKER, W. J. (1843), p. 500.

‡ LAMBERT (1803), Appendix, p. 88.

§ ANTOINE (1847), Plates 38-42.

|| GARDNER (1881).

¶ For illustrations see LINDLEY (1851), HOOKER, W. J. (1852), 'Gard. Chron.' (1888), p. 774; (1901), p. 387; BRONGNIART and GRIS (1871).

\*\* 'Gard. Chron.' (1888), p. 774, fig. 104. See also 'Gard. Chron.' (1901), p. 387 (November 30); the photograph of the top of the tree in the Temperate House at Kew (since cut down) was originally taken for one of us to illustrate the female cones in the first, second, and third year (reproduced in fig. 12).

†† LINDLEY (1851), p. 267; DON (1841), p. 164.

The leaves are similar to those of *A. Cunninghamii* and *A. excelsa*; on the main axis they are more curved and freer than on the lateral shoots, on which they are broader and more imbricate. In the variety *luxurians*\* (fig. 11, A), found in association with the type at Kanala, the leaves reach a length of 8–9 millims., and closely resemble those of *A. montana*. The plant referred to by VIEILLARD as *A. intermedia*, from Kanala (fig. 11, B), is no doubt specifically identical with *A. Cookii*. The drawing (fig. 11, B) was made from a specimen in the Kew Herbarium, obtained from VIEILLARD'S collection.

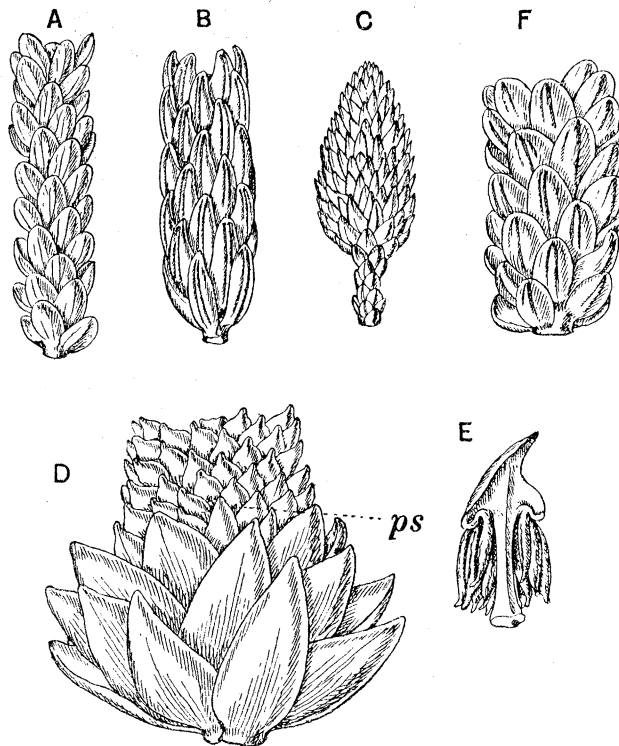


FIG. 11.—A, *Araucaria Cookii*, var. *luxurians*; B, *A. Cookii* (= *A. intermedia*, Vieill.); C, *A. Cookii*, male flower; D, E, *A. Muellieri*, p.s. = pollen-sacs; F, *A. Montana*. ( $\frac{1}{2}$  nat. size.)

The male flowers are subcylindrical (5–8 centims.  $\times$  1.5 centims.), showing a gradual transition from foliage leaves to sporophylls† (fig. 11, c) bearing 10 pollen-sacs. The female cones, which take three years to ripen (fig. 12), are very similar to those of *A. Cunninghamii*; the winged cone-scales (fig. 24, g) terminate in a comparatively long linear appendage.

The seedlings are of the same type as those of *A. excelsa* and *A. Cunninghamii*, and are characterised by a slender axis, spreading needle-like leaves and epigeal cotyledons.

\* BRONGNIART and GRIS (1871), p. 132.

† THIBOUT (1896).



FIG. 12.—*Araucaria Cookii*, Cones in three stages of development.

*Araucaria Rulei*. Figs. 13, A ; 20, B-D, F-H ; 22 ; 25, A-C ; 26, A.

1861. *Araucaria Rulei*,\* 'Gard. Chron.', p. 868, figs. 1-6.

This species (introduced 1862) was discovered by Mr. DUNCAN, a botanical collector to Mr. JOHN RULE, of Melbourne, on a lofty volcano on an island near New Caledonia.†

The leaves (2 centims. long, 5 millims. to 1 centim. broad) (fig. 20, B-D) are arranged in a dense spiral, and have the falcate form of those of the Norfolk Island Pine, but differ in their larger size and in the broader and flatter lamina, which has a fairly well-marked keel on the lower surface. The vegetative shoots of this species constitute a type intermediate between that represented by *A. excelsa*, *A. Cookii*, and *A. Cunninghamii*, on the one hand, and *A. imbricata* on the other.

\* For illustrations see 'Gard. Chron.' (1861), p. 868: 'L'Illus. Hort.,' vol. 22, Plate 204; BRONGNIART and GRIS (1871).

† 'Gard. Chron.' (1861), p. 868; VEITCH (1900), p. 305.

The male flowers may attain a length of 24 centims. (fig. 13, A). Each sporophyll bears 15 pollen-sacs. The female cones are similar to those of *A. Cookii*.

*Araucaria Balansa*. Fig. 20, I.

1871. *Araucaria Balansa*,\* BRONGNIART and GRIS, 'Bull. Soc. bot.,' xviii, p. 130, and 'Nouv. arch. Mus.,' vii, p. 206, Plate 13.

A New Caledonian tree originally described by BRONGNIART and GRIS from specimens collected by M. BALANSE as reaching a height of 40–50 metres, and growing at an altitude of 500 metres.†

The leaves are ovate-triangular or subtetragonal in form, 4–5 millims. long and 2·5 millims. in breadth; of similar type to those of *A. Cookii*.

The male flowers (3–5 centims. long and 1·5 centims. broad) bear sporophylls with 10 pollen-sacs arranged in two rows. The female cones (10–11 centims. × 7–8 centims.) have an elliptical or globose form.

*Araucaria Muelleri*. Figs. 11, D, E.

1867. *Araucaria Muelleri*,‡ CARRIÈRE, 'Conif.,' p. 607.

*Illustrations*.—BRONGNIART and GRIS, 1871. Branches and cones.

*Araucaria Muelleri*.—CARRIÈRE§ has expressed the opinion that this New Caledonian type is identical with *A. Rulei*, as described in the 'Gardeners' Chronicle,'|| but we see no sufficient reason for adopting this view. The garden-form of *A. excelsa* figured as *A. Muelleri* Hort. in the 'Illustration Horticole,'¶ must not be confounded with *A. Muelleri* of BRONGNIART and GRIS. The leaves are ovate-imbricate (3 centims. × 2 centims.), resembling those of *A. Rulei* and *A. imbricata*.

The male flower is of unusual length (fig. 11, D, E) in some cases 25 centims. with a breadth of 3–4 centims. The sporophylls bear as many as 20 pollen-sacs (fig. 11, E).

The female cones (14 × 9 centims.) resemble those of *A. Rulei*. In both the female and male shoots the foliage leaves pass gradually upwards into the sporophylls.

\* For illustrations see 'L'Illust. Hort.' (1875), vol. 22; BRONGNIART and GRIS (1871).

† BRONGNIART and GRIS (1871), p. 130; (1871<sup>2</sup>) p. 206.

‡ For illustrations see BRONGNIART and GRIS (1871).

§ CARRIÈRE (1867), p. 607.

|| 'Gard. Chron.' (1861), p. 860.

¶ Vol. 29, p. 449.

*Araucaria montana.* Fig. 11, F.

1871. *Araucaria montana*, BRONGNIART and GRIS, 'Nouv. arch.,' vii, p. 215, Plate 14, figs. 1-3; and 'Bull. Soc. Bot.,' xviii, p. 136.

This species, also from New Caledonia, was recorded by BRONGNIART and GRIS at an altitude of 1000 metres. The shoots (fig. 11, F) are similar in appearance to those of *A. Cookii* var. *luxurians*, with leaves of  $1.3 \times 8$  millims.

The male flowers (8-9 centims.  $\times$  2-3 centims.) are considerably smaller than those of *A. Muelleri*; the sporophylls are said to bear 12 pollen-sacs.

## c. DOUBTFUL SPECIES.

*Araucaria Saviana.*

In 1861 PARLATORE\* described a plant found near Cobijan in the Bolivian mountains as *A. Saviana*, which he regarded as a species distinguished from *A. brasiliensis* by certain features in the cones. Such differences as he mentions seems hardly sufficient to justify the institution of a new species.

*Araucaria subulata.*

A species created by VIEILLARD† for a tree met with in the valleys of New Caledonia; it is described as differing from *A. Cookii* in having a trunk less denuded of branches and in its linear subulate leaves. VIEILLARD's plant is probably identical with *A. Cookii*; the resemblance to this species has been noticed by CARRIÈRE.‡

*Araucaria Grayi.*

Under this name BARON VON MUELLER§ mentions a species found within a circumscribed area on the Glenelg River in North Australia.

## IV. SEEDLINGS.||

Our examination of seedlings has been confined to a few species of the genus *Araucaria*.

*A. External Form.*—(a) Sect.: COLYMBEA. Descriptions of the germination of *Araucaria Bidwillii* have been published by DÜRER,¶ and more recently by BLANCHARD\*\* and HECKEL.†† At an early stage in germination the young axis

\* PARLATORE (1861), p. 89.

† VIEILLARD (1862), p. 89.

‡ CARRIÈRE (1867), p. 614.

§ MUELLER (1867), p. 8.

|| The anatomy of coniferous seedlings will be dealt with to some extent by Mr. A. G. TANSLEY and Miss E. N. THOMAS, in a forthcoming publication on the vascular anatomy of Dicotyledonous and Gymnospermous hypocotyls.

¶ DÜRER (1865).

\*\* BLANCHARD (1892).

†† HECKEL (1892).

becomes considerably swollen and assumes a carrot-like form (fig. 13, B); the stalks of the cotyledons form a closed tube, which grows in length and embraces the plumule; subsequently the cotyledonary tube is cut off near the base of the plumule by a ring of cork. After the fall of the cotyledons the seedling may remain in a resting

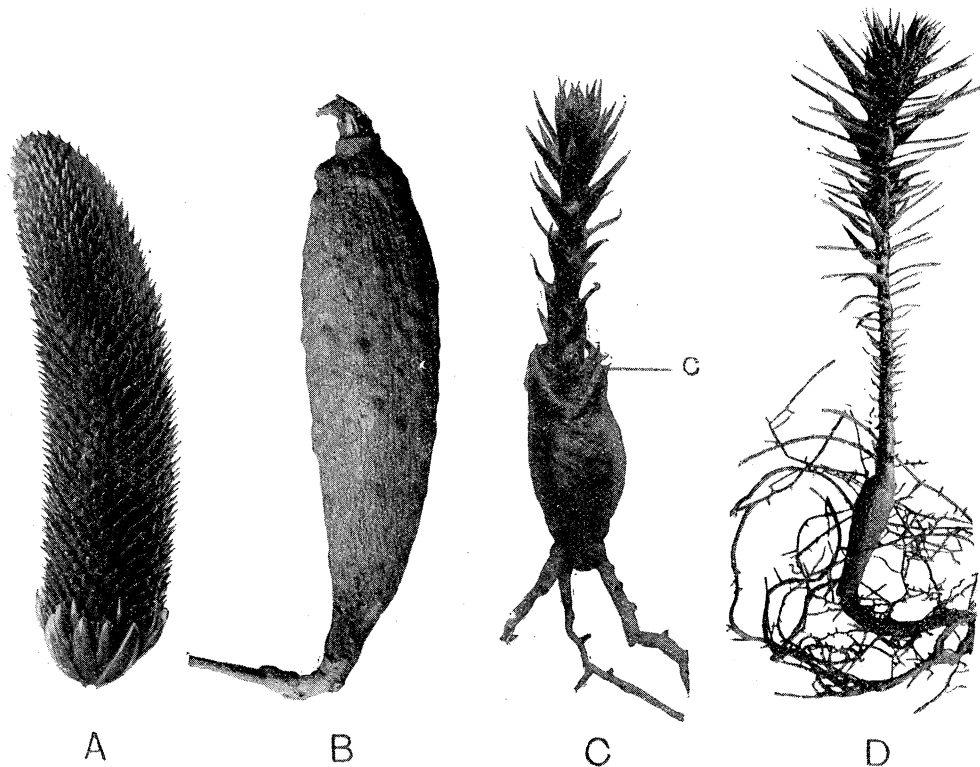


FIG. 13.—A, *Araucaria Rulei*, male flower ( $\frac{1}{2}$  nat. size); B, *A. Bidwillii*, seedling; C, D, *A. imbricata*. (B—D nat. size.)

condition; in this state it is capable of resisting drought, and may be sent to Europe without losing its power of germination. It has been suggested that the first stage of germination may correspond with a short rainy season, while the resting stage coincides with a period of drought. DÜRER\* figures an example of a young seedling which formed two plumular shoots, and after being split into half produced two plants. In 1901 some seedlings of *A. Bidwillii* were sent to Kew by Mr. E. TIDMARSH, the Curator of the Botanic Gardens, Grahamstown, which were briefly described by Mr. HEMSLEY† at a meeting of the Linnean Society of London. We are indebted to the Director of Kew for affording us an opportunity of examining one of these seedlings. Mr. TIDMARSH, in a letter to Sir WILLIAM THISELTON-DYER (August 19, 1901), states that he germinated some of the “wooden carrots” recovered from a wrecked vessel. He notes that the plumule began to elongate

\* DÜRER (1865), figs. 4 and 5.

† HEMSLEY (1902).

a few weeks after the fall of the cotyledons : it would seem therefore that a prolonged interval is not essential.

In *Araucaria imbricata* two cotyledons are normally produced as in *A. Bidwillii*, but, as shown in some of RICHARD's figures,\* one and three also occur. MASTERS† has published figures of seedlings, and LOUDON‡ has also given drawings of germinating seeds. On pulling to pieces a large cone of *A. imbricata* we found that several of the seeds had begun to germinate, and in one case a radicle 1 centim. long had penetrated between the axis of the cone and the cone-scales. This precocious germination suggests a comparison with the young plants described by Miss LYON§ on the strobili of *Selaginella rupestris*. With the assistance of Mr. LYNCH, of the

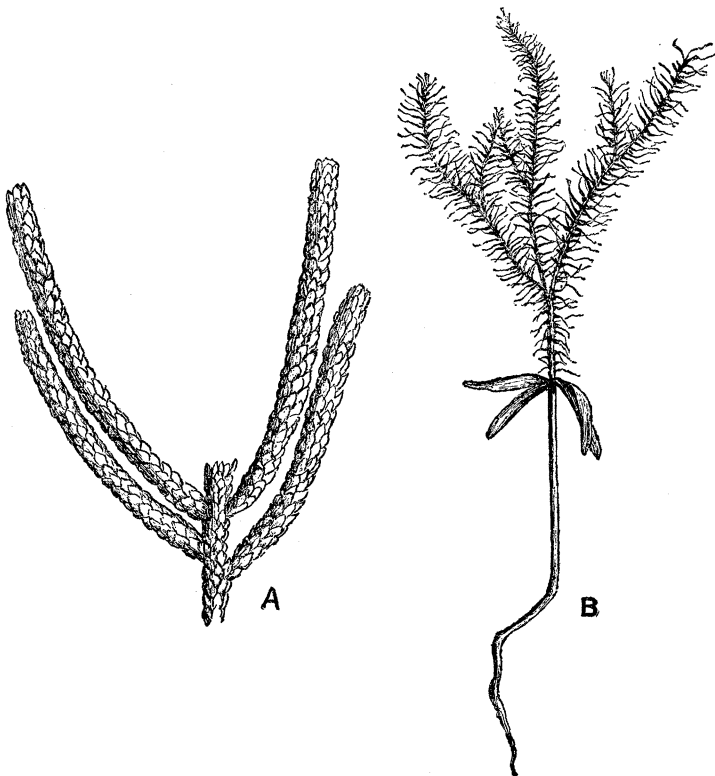


FIG. 14.—*Araucaria excelsa*, A, mature form ; B, seedling.  
(From a block lent by the University Press, Cambridge.)

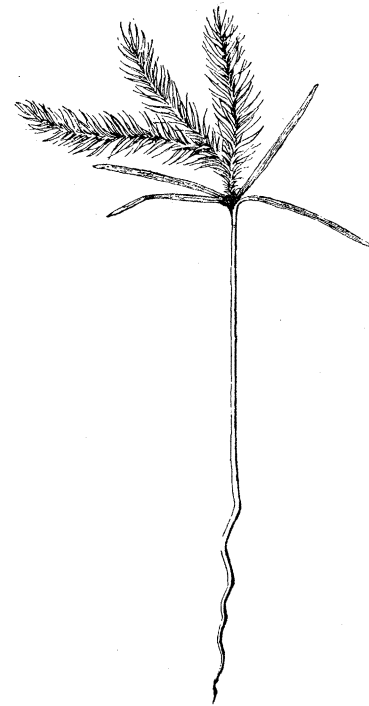


FIG. 15.—*Araucaria Cookii*.  
( $\frac{1}{2}$  nat. size.)

Cambridge Botanic Garden, we were able to obtain several young plants in different stages (figs. 13, c and d). As in *A. Bidwillii* the hypocotyl forms a food-reservoir, the cells of the broad pericycle being packed with starch, but it does not reach the thickness attained by the Australian species. The remains of two cotyledons are seen at C in fig. 13, c, at the upper end of the swollen axis ; fig. 13, d, shows

\* RICHARD (1826), Plate 20.

† MASTERS (1891), p. 234, figs. 2 and 3.

‡ LOUDON (1875), p. 1065.

§ LYON (1901).



a gradual transition from the small scale-leaves at the lower end of the epicotyl to the adult leaf, and the two buds at the apex represent the first stage of branching.

(b) Sect. : EUTACTA.—The species of this section produce seedlings of a type very different from those of the *Colymbea* group. The axis is slender and bears four linear cotyledons. Figures of embryos and seedlings of *Araucaria excelsa* have been published by ANTOINE\* and LAMBERT.† The example from the British Museum Herbarium represented in fig. 14, B, is one named by ROBERT BROWN; the older shoot shown in fig. 14, A, illustrates the striking difference between the young and old foliage, a difference not met with in the *Colymbea* species. The seedling of *A. Cookii* from Port Bowen (Brit. Mus. Herbarium, ROBT. BROWN, 1802) represented in fig. 15 agrees very closely with that of *A. excelsa*, and between these species and *A. Cunninghamii* there is an equally close resemblance.

*B. Internal Structure.*—The following account, which has reference only to *A. imbricata* and *A. Bidwillii*, is chiefly based on the examination of seedlings of the former species having an unbranched epicotyledonary axis 11 centims. in length, and a swollen hypocotyl 3 centims. long (slightly younger than the seedling shown in fig. 13).‡

Fig. 16, A, represents a section of a diarch root of *A. imbricata* 1 millim. in diameter, in which the xylem occurs as two short plates; on the flanks of the conjunctive parenchyma *cp.* (figs. 16, A and A<sup>1</sup>) there are two crescentic areas of larger and clear cells *b*, some of which probably represent the primary phloem. The pericycle, *Pr*, consists of several layers of cells traversed by 10 resin-canals (*c*) and bounded by an endodermis *e*, characterised by radial thickenings and deeply stained contents. The cortical layer abutting on the endodermis also possesses similar suberised thickenings, and the cells of the second and third layers of the cortex next the superficial layer exhibit small suberised patches at the angles. In the sections described below, the surface is formed of cork-tissue produced at an early stage immediately internal to the endodermis. At a slightly higher level than that represented by fig. 16, A, some of the cells in the areas *b* (figs. 16, A) become the seat of meristematic activity, resulting in the production of two crescentic groups of secondary xylem (fig. 16, B, *x*<sup>2</sup>), which do not extend across the gaps opposite the protoxylem until a later stage. The region *p* is occupied by cambium and secondary phloem. The xylem plates have now become broken up into separate tracheal strands *x*<sup>1</sup>. The areas *b*, in fig. 16, B, consist of large cells succeeded internally by secondary phloem and limited on the outside by an irregular line of crushed cells, *cr*. The tissue *b* does not, however, differ from the rest of the

\* ANTOINE (1847), Plate 38.

† LAMBERT (1803), Appendix, Plate 39.

‡ Cf. LYON (1904); CHICK (1903). The structure of the Araucarian seedlings is of a different type from those described in *Ginkgo* and *Torreya*.

pericycle, and the limiting lines shown in the diagrams do not denote a boundary of morphological importance. In the diagrams B and C the endodermis, *e*, forms the limiting line. The next stage is represented by fig. 16, C (3 millims. in diameter);

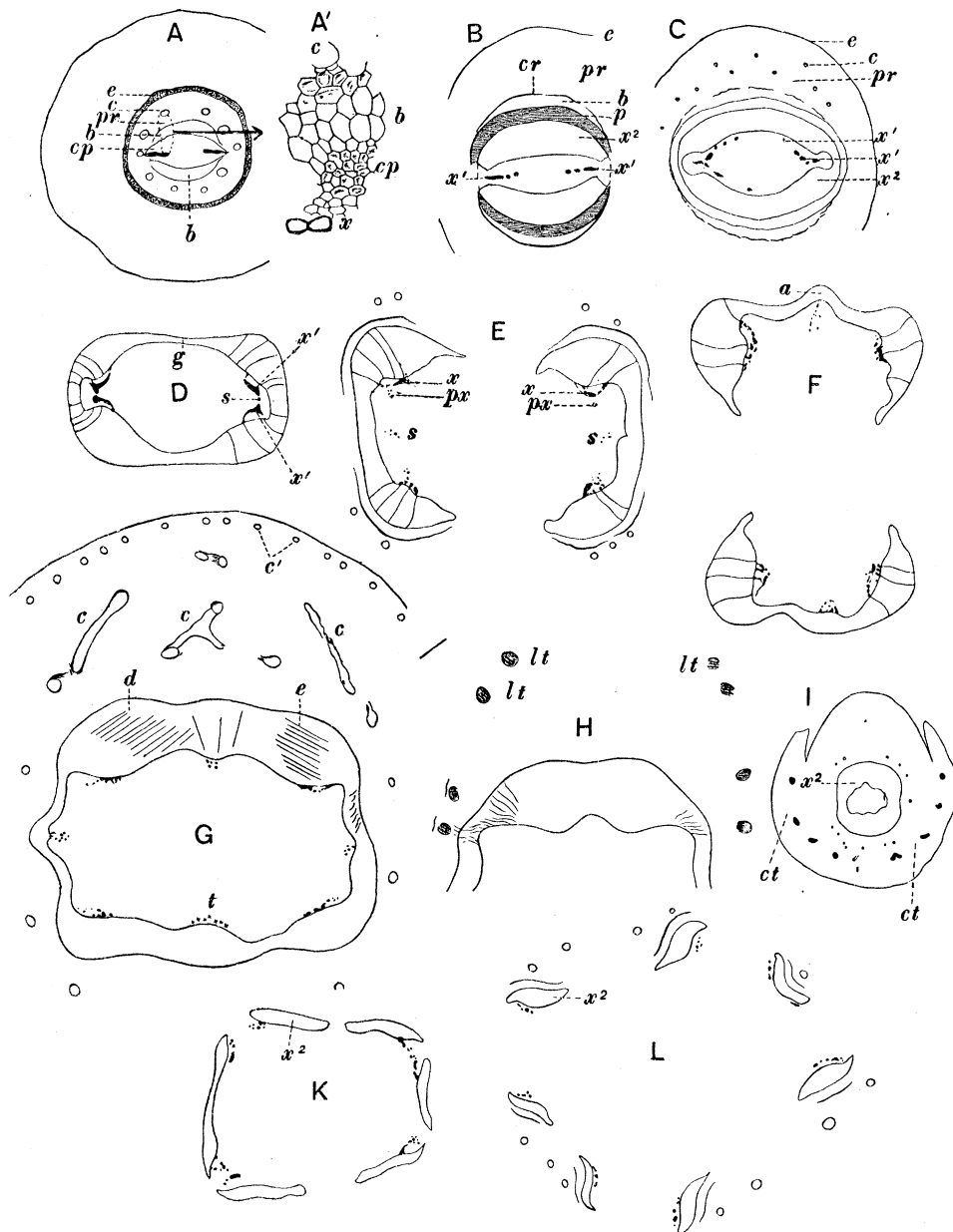


FIG. 16.—*Araucaria imbricata*. Diagrams showing the anatomy of seedlings.

the two primary xylem plates have undergone a further subdivision, and the scattered metaxylem elements,  $x^1$ , are seen close to the inner edge of the secondary wood, which is now continuous across the two bays occupied by conjunctive-tissue and protoxylem. The broader pericycle, *pr*, contains an increased number of secretory canals, *c*.

The stele may next assume a triarch structure by the splitting of one of the protoxylem strands, or by the division of both strands it may pass directly into the form shown in fig. 16, D. The isolated groups of metaxylem tracheids ( $x^1$ , fig. 16, c) have now disappeared; the bays, which have become wider, contain two groups of primary xylem each ( $x^1$ ) with a few additional spirally thickened elements (*e.g.*, *s*, fig. 16, D); the main strands are curving away from one another and some of the metaxylem elements are brought into continuity with the inner edge of the secondary xylem. A further change is seen in the gradual decrease in thickness of the secondary xylem at *g*, which is continued until a gap is formed, and at a slightly later stage a corresponding gap appears on the opposite side of the stele (fig. 16, E); the section of which a portion is shown in fig. 16, E, has a long diameter of 1.4 centims. The two bays have increased in breadth, and a few spiral elements are seen at *s* in the middle of each. The protoxylem elements, *px*, are becoming obliterated, with the formation of irregular gaps in the adjoining tissue; the metaxylem tracheids, *x*, form a curved band continuous with those of the secondary xylem. The secondary xylem bands, which in fig. 16, E, have the form of broad and flat arches, now curve outwards to form subsidiary arches, *A*, in the middle of each bay (fig. 16, F). In addition to the numerous canals in the pericycle others have been produced immediately internal to the phelloderm (fig. 16, G, *c'*), recalling the secretory canals in the outer cortex of certain Lepidodendroid stems. The secondary xylem as seen in fig. 16, G, has again become continuous; as in the previous section, there are six protoxylem groups: at *t* on the inner edge of the secondary xylem occurs a group of large and more or less isodiametric elements identical, in form and in their reticulate pitting, with transfusion tracheids: in the corresponding position on the opposite side of the pith a few crushed protoxylem elements are seen, but in a section cut at a slightly lower level larger tracheids occur identical with those at *t*. The tracheids of the secondary xylem at *d* and *e* appear to be bending out in an almost horizontal plane, and the canals *c* on that side the xylem pursue a similar course. At a higher level bundles (fig. 16, H *lt*) become detached from the xylem-ring and subdivide in the pericycle as they pass to the two cotyledons. A slightly later stage is represented by fig. 16, I, which shows a complete section with the fused cotyledonary stalks, *ct*, traversed by eight vascular bundles and a xylem cylinder,  $x^2$ , of reduced size. A section above the cotyledons presents an appearance similar to that of fig. 16, I, as regards the stele, which consists of a tube of secondary xylem with a slightly crenulated inner margin, from which leaf-trace bundles are given off.

In another seedling of *Araucaria imbricata* we found that the behaviour of the vascular tissue differed in some respects from that already described. In the lower part of the swollen axis the stele was tetrarch as in fig. 16, D; by the bifurcation of the protoxylem strands and the splitting of the secondary xylem-band the form represented in fig. 16, K, was produced, and this at a still higher level assumed the

arrangement shown in fig. 16, L. Finally, a continuous ring was again formed as in the seedling previously described.

In the seedling of *A. Bidwillii* the stages were found to agree with those in *A. imbricata* (as represented by figs. 16, D, K, L), and the section represented in fig. 16, L, would serve equally well to illustrate the structure of the Australian species.

The chief results obtained are (i) the practical identity in structure of the seedlings of the two species of *Araucaria*, *A. Bidwillii*, and *A. imbricata*; (ii) the increase in size of the pericycle to form a food-reservoir; (iii) the abundance of secretory canals in the food-storing tissue; (iv) the breaking up of the xylem and the increase in width of the vascular network in the thickest part of the hypocotyl; (v) the disappearance of all traces of the primary xylem of the root at the level of exit of the cotyledonary bundles; (vi) the continuity of the cotyledonary stalk with the pericycle tissue of the hypocotyl.

## V. STEM ANATOMY.

### a. *Apex and Young Stem.*

Our examination of the apical regions of stems of the *Araucariæ* has been confined to those of *Agathis robusta*, *Araucaria imbricata*, and *A. Bidwillii*. Neither in lateral branches nor in the main stem have we found any indication of the presence of a single apical cell: a fairly well marked dermatogen may usually be recognised, but no well-defined boundary separates a periblem from a plerome region. The structure was found to be more in accord with Koch's descriptions\* than with the conclusions of DOULIOT.†

A transverse section through the apex of a lateral branch of *Agathis robusta* shows the central axis consisting of a fairly large pith surrounded by desmogen strands and encircled by a few scale-leaves in continuity with or detached from the stem tissues. Five lateral apices identical in structure with the central axis surround the young stem. The apical cone agrees closely in shape with that of *Araucaria imbricata* represented in Plate 24, fig. 17, A. In *A. imbricata* the divergent desmogen-tissue encloses a wide pith region, but the boundary between extra- and intra-stelar tissues is ill-defined. A transverse section through the apex shows a mosaic of leaves closely investing the central apex. A young leaf examined at the stage when a few tracheids have become lignified is found to be traversed by a single collateral bundle; the mesophyll contains several resin-canals in various stages of development, and a few partially thickened idioblasts are already apparent. Fig. 18, A, represents a leaf-

\* KOCH (1891).

† DOULIOT (1890). For references to the controversial subject of the structure of the apices of Gymnosperm stems, see DE BARY (1884), p. 14; STRASBURGER (1872), p. 324; SKROWISZEWSKI (1873), p. 448; DINGLER (1882), p. 795; KORSCHULT (1884), p. 642; GROOM (1885); and SCOTT (1894).

bundle with a few protophloem, *pp*, and protoxylem, *px*, elements; the larger cells beyond the protoxylem (fig. 18, A, *cp*) are probably destined to form the strand of centripetal tracheids. The precocious development of the resin-canals in the young stem and leaf-tissue constitutes a striking feature in the Araucarieæ.

A stem of *A. imbricata* as seen in a transverse section near the apex contains a large pith surrounded by a cylinder of desmogen strands succeeded by a broad zone of cortex and confluent leaf-bases; in the inner part of the extrastelar region the leaf-trace bundles occur in various stages of branching, and farther out the position of each leaf is clearly defined by a row of bundles and a series of canals with very large lumina.

The broad pith, which in the apical region consists entirely of lacunar parenchyma, soon develops numerous sclerites of an irregular branched form, and these eventually occupy a considerable proportion of the pith-tissue. In the region of lateral branches the pith-cells assume a stellate form with short arms and bluntly rounded ends, which are constricted off as the branch-cylinders become free from the stele of the main axis.

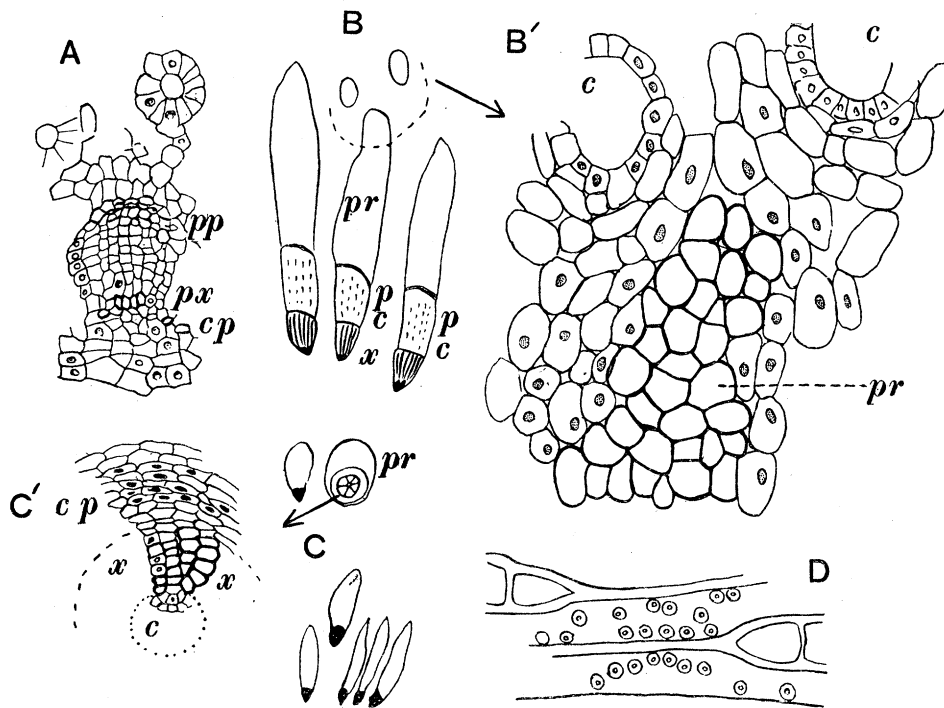


FIG. 18.—*Araucaria imbricata*. A—C, young stem; D, tangential section of older wood.

The vascular ring of the young stem consists of numerous narrow bundles elongated in a radial direction and characterised by a broad meristem-zone and by the occurrence of a group of comparatively small and thin-walled cells external to the protophloem. Three bundles are represented in outline in fig. 18, B, showing the

relative size of the xylem ( $x$ ), cambium, and phloem ( $c$  and  $p$ ), and accompanying pericycle tissue ( $pr$ ), which eventually becomes converted into thick fibres.

The enlarged drawing shows the structure of the pericycle tissue ( $pr$ ), and demonstrates the continuity between the medullary-ray cells with those of the cortex without the occurrence of an endodermal layer. Fig. 18, c, illustrates the occurrence of a concentric vascular strand in the cortex of a young stem of *A. imbricata*: this consists of a few thin-walled, central cells, fig. 18, c, c, completely surrounded by a ring of tracheids,  $x$ , traversed by a few medullary rays and succeeded by a broad zone of cambium and young phloem elements ( $c$  and  $p$ ). The pericycle cells, as shown at  $pr$ , fig. c, do not form a complete investment. We prefer to regard this concentric strand as a leaf-trace of unusual structure rather than attribute to what is undoubtedly an exceptional occurrence any morphological significance.

The cortex of the young stem is composed of lacunar parenchyma penetrated by a very large number of canals and traversed by leaf-traces in different stages of branching. As seen in Plate 24, fig. 17, B, the leaf-traces carry with them from the vascular ring a strand of extra-phloem tissue or pericycle, which may assume a crescentic form ( $pr$ ), and in the young condition, before the cells have become fibrous, this tissue bears a striking resemblance to the parichnos of *Lepidodendron*.<sup>\*</sup> The form and position of this tissue, as seen at  $pr$ , are almost identical with the parichnos of a *Lepidodendroid* leaf-trace. Sclerites occur abundantly in the cortex, more especially in the zone of tissue at the broad bases of the leaves at their junction with the stem, a position where the occurrence of thick-walled elements may serve to give flexibility and cohesion to the tissues.

A similar type of structure is met with in the young stem of *A. Rulei*; a broad pith crowded with lignified and crystal-studded sclerites is surrounded by a vascular ring with leaf-gaps. The cortex consists of large-celled lacunar parenchyma with sclerites and branching leaf-trace bundles, accompanied on their outer face by a strand of fibres.

#### b. OLD STEMS.

The genera *Araucaria* and *Agathis* possess anatomical characters which were first recognised by NICOL and WITHAM<sup>†</sup> as distinguishing features of living Araucarieæ, and of certain Carboniferous trees. DON,<sup>‡</sup> who instituted the group Araucarieæ, noticed the agreement between *Araucaria* and *Agathis* in the possession of contiguous rows of hexagonal, bordered pits in contrast to the single rows of circular pits in the wood of *Cunninghamia*, which he included with hesitation in the

<sup>\*</sup> Cf. SEWARD (1899), Plate 3.

<sup>†</sup> GÖPPERT (1881).

<sup>‡</sup> DON (1841), p. 163.

same group. In 1862 SCHACHT\* published an account of the anatomy of *Araucaria brasiliensis*, and since then numerous contributions have been made to our knowledge of the anatomy of the Araucarieæ.

The two genera *Araucaria* and *Agathis* agree so closely with one another, and indeed KRAUS† states it is practically impossible to distinguish one from the other, that they may be treated as a single anatomical type. For a more detailed account of the anatomy of the Araucarieæ reference should be made to the third volume of STRASBURGER's *Histologische Beiträge*,‡ and to the recently published monograph by PENHALLOW.§

The most striking anatomical features of the Araucarieæ may be described as follows :—

Annual rings are well-marked in some stems but absent or feebly developed in others. Divergent statements have been made with regard to the presence or absence of well-defined rings of growth in the stem wood of the Araucarieæ. SCHACHT|| describes *A. brasiliensis* as having rings, and STRASBURGER¶ speaks of them as very faintly marked, but recognisable microscopically and by the occurrence of pits on the tangential walls of the late summer tracheids. DE BARY\*\* mentions clearly marked rings in *Araucaria excelsa*, but recognises a lack of uniformity in this character. We found the annual rings clearly defined in the old tree of *A. imbricata* from Kew (Plate 24, fig. 17, c), but their presence in wood grown in England cannot be accepted as a satisfactory proof of their occurrence in Chilian trees. In the stem of *A. Bidwillii* from the temperate house of the Cambridge Botanic Garden rings were found to be absent or very feebly marked. No distinct rings were found in the examples of *A. excelsa* which we examined. The following figures serve to illustrate the range of variation in the size of the tracheids in the spring and late summer wood, as well as the difference between the newer and older wood: the measurements represent the average diameters in micromillimetres, calculated from groups of tracheids in the same region. The figures demonstrate that there is, roughly speaking, a decrease in the radial diameter of the tracheids from the peripheral region towards the pith. The diameters of the tracheids in the root included in the following table are considerably larger than in the stem elements. In lateral branches the elements are smaller than in the main stem.

\* SCHACHT (1862).

† KRAUS (1864).

‡ STRASBURGER (1891).

§ PENHALLOW (1904).

|| SCHACHT (1862), p. 410.

¶ STRASBURGER (1891), p. 87.

\*\* DE BARY (1884), p. 8.

Species.	Region of tree.	Spring wood.		Latest-formed Summer wood.	
		Diameter between tangential walls.	Diameter between radial walls.	Diameter between tangential walls.	Diameter between radial walls.
<i>Araucaria imbricata</i>	I. Stem.				
	A. Old tree trunk from Kew, 60-70 annual rings—	$\mu$ .	$\mu$ .	$\mu$ .	$\mu$ .
	(1) Near pith . . . . .	26	25.9	6	15
	(2) 2-3 inches from periphery . . . . .	29	25.6	8.6	22
	(3) Near periphery . . . . .	30	26	7.6	18
	B. Younger tree from Kew—				
	(1) Immediately below apex, primary wood only	10.3	10	—	—
	(2) Wood of 2nd annual ring in stem of two years' growth	25.6	21.6	6.6	17
	(3) Wood of 8th annual ring in stem of about eight years' growth	29.6	25	9	18.6
	II. Branch.				
	(1) Lateral branch . . . . .	16	14.3	6	14
	(2) Small accessory lateral branch. . .	13.6	13.6	6	13.6
	III. Root.				
	(1) Secondary wood of 1st and present year	30.3	22.3	—	—
	(2) Secondary wood from root of several years' growth, near the periphery	46.3	31.6	13	30.6
<i>Araucaria Bidwillii</i>	I. Stem.				
	Tree from Botanic Garden, Cambridge, cut down July, 1901—				
	(1) Base of the tree and near the pith .	32.3	24	Not clearly distinguished.	
	(2) Stem of several years' growth, midway between pith and periphery	35.6	28.6		
	(3) Stem of three years' growth . . .	37	24.6	12	14
	(4) Immediately below apex, primary wood only	14.6	17.3	—	—
	II. Branch.				
	Lateral branch of two years' growth .	19.6	13.6	8.1	7
	III. Root.				
	(1) Secondary wood of 1st year only. .	60.6	38	—	—
	(2) Secondary wood from root of several years' growth	38.6	33	19	21.6



Species.	Region of tree.	Spring wood.		Latest-formed Summer wood.	
		Diameter between tangential walls.	Diameter between radial walls.	Diameter between tangential walls.	Diameter between radial walls.
<i>Araucaria excelsa</i>	I. Stem from Kew.	μ.	μ.	μ.	μ.
	(1) Immediately below apex, primary wood only	11·5	9·8	—	—
	(2) Stem of several years' growth—				
	(a) Near periphery . . . . .	29·3	31·6	11·6	30·6
<i>Araucaria Cookii</i>	(b) Near pith. . . . .	27·6	28·6	13	26·3
	I. Stem from Kew.				
	Wood of several years' growth . . . .	33·3	29·6	16	19·3
	II. Branch.				
<i>Agathis robusta</i>	Lateral branch below cone . . . . .	15·6	13·6	8·6	8·3
	From the Botanic Garden, Cambridge, cut down October, 1901—				
	I. Stem.				
	(1) Primary wood immediately below apex	19	17·5	—	—
	(2) Secondary wood of 1st year . . .	33	25·6	—	—
	(3) Secondary wood of several years' growth	36·3	23·3	15·3	14·6

In the species of *Agathis* similar differences occur in regard to the distinctness of the rings of growth. STRASBURGER\* mentions well-marked rings in *Agathis australis*, whereas in *A. robusta* the rings are either absent or very faintly marked.

The pith is unusually large and is characterised by the abundance of large branched sclerites. The inner edge of the wood, as seen in radial section, consists of partially destroyed tracheids which are represented by crushed and extended double spiral threads; these are succeeded by several tracheids with walls intact and characterised by a close spiral band, while beyond these the xylem elements possess bordered pits in addition to the delicate spiral bands. The inner edge of the wood constitutes a fairly broad zone—consisting of spiral tracheids, tracheids with a single row of oval pits and others with both spiral bands and small bordered pits—which recalls the broad transitional region in the stems of the Palæozoic *Cordaite*s.

The secondary wood is composed of tracheids with a single or double row of

\* STRASBURGER (1891), p. 89.

contiguous pits on their radial walls, and occasionally with three or four rows\* of spirally disposed polygonal pits.† As is usually the case in conifers without horizontal tracheids in the medullary rays, pits occasionally occur on the tangential walls of the tracheids of the late summer wood; in both *Araucaria* and *Agathis* these pits have a smaller diameter than those of the radial walls. The following table gives the average diameters (estimated in micro-millimetres) of the bordered pits on the radial and tangential walls of species of *Araucaria* and of *Agathis robusta* :—

Species.	Region of tree.	Diameter of pits on radial walls (Spring wood).	Diameter of pits on tangential walls (latest-formed Summer wood).
<i>Araucaria imbricata</i> .	Stem . . . .	μ. 15	μ. 8·3
	Root . . . .	13	10
<i>Araucaria Bidwillii</i> .	Stem . . . .	14	10·3
	Root . . . .	14·3	12·3
<i>Araucaria Cookii</i> . .	Stem . . . .	15	7·3
<i>Araucaria excelsa</i> . .	Stem . . . .	14	11·6
<i>Agathis robusta</i> . . .	Stem . . . .	15	8·6

Fig. 18, D (p. 337), illustrates the irregular occurrence of numerous pits on the tangential walls of *Araucaria imbricata*. PENHALLOW speaks of tangential pits in *Agathis*, but he does not appear to have observed any in *Araucaria*.

In some sections of the wood of *A. imbricata* we noticed tracheids in which the cavity was occasionally bridged across by a thick cross-bar.‡

In sections of old Araucarian wood the tracheids often show very clearly marked spiral lines which have doubtless been produced by enzymes; the path of the solvent agent becomes filled with air and renders the spiral lines very distinct.

Most authors speak of xylem-parenchyma as a constituent of Araucarian wood, but an examination of numerous sections of the wood of several species leads us to confirm PENHALLOW's statement§ that the so-called parenchymatous elements are in reality tracheids in which a peculiar deposit of resin simulates the cross-walls of parenchymatous cells.

The medullary rays are long and narrow, as seen in a radial longitudinal section, with the upper and lower walls slightly arched. KLEEGER|| states that these

\* ZITTEL (1890), p. 851.

† PENHALLOW (1904), p. 258. See also STRASBURGER (1891), p. 88.

‡ STRASBURGER (1891), p. 33.

§ PENHALLOW (1904), pp. 523 *et seq.*

|| KLEEGER (1885), p. 693. See also EICHLER in ENGLER and PRANTL (1889), p. 36.

elements are destitute of pits, but we find that faintly bordered pits are fairly numerous on the walls of the ray-cells. The lumina of medullary-ray cells occasionally contain a resinous secretion. The medullary rays, as seen in a tangential section of Araucarian wood, consist of a single row of cells varying in depth from 1–20 cells; in *Agathis robusta* we noticed an occasional ray two cells in breadth.

The cambial zone is of considerable breadth; in sections of *Araucaria imbricata* there may be as many as 20 cells in a radial row between the lignified wood and the phloem.

The phloem\* consists of sieve-tubes with plates on the radial walls, particularly well shown in *A. excelsa*, and of albuminous cells with long thick-walled fibres, studded with calcium oxalate crystals, and scattered secretory cells. Fibres are particularly abundant in *A. excelsa* and fewer in *A. Bidwillii* and *A. imbricata*; in the latter species EICHLER† speaks of them as absent. SOLMS-LAUBACH has described the occurrence of calcium oxalate crystals in the cell-walls of *Araucaria excelsa*.‡

The cortex is composed of parenchymatous tissue with numerous canals, branched sclerites, and fibres; in some species (e.g., *A. excelsa*) nests of thick-walled cells form a conspicuous feature. Long and narrow fibres occur abundantly in the cortex; internal to the shell of bark of an old tree of *Araucaria imbricata* we found fibres reaching a length of 3–4 millims., forming a loose dust weathered out of the less resistant tissues.

The formation of cork in the Araucarieæ is described by BERTRAND as usually taking place in the third or fourth year; in sections of *Agathis* stems several years old we noticed that no phellogen had been developed.

## VI. Roots.

Our examination of the roots of the Araucarieæ has been confined to those of *Araucaria imbricata* and *A. Bidwillii*. The normal structure of the roots does not differ in any striking respects from that met with in other members of the Coniferales, but there are a few points which are perhaps worthy of mention.

*Araucaria Bidwillii*.—The young root of this species has a diarch stele with a continuous plate of primary xylem. The broad pericycle contains several large and thick-walled elements and some secretory canals; at an early stage in the growth of the root rows of secondary xylem tracheids are produced on either side of the metaxylem plate, and the outer limit of the pericycle is represented by several layers of cork. We may conveniently adopt the terms fascicular and inter-

\* STRASBURGER (1891), Plate 2, figs. 30–38.

† EICHLER in ENGLER and PRANTL (1889), p. 36.

‡ SOLMS-LAUBACH (1871), Plate 6, fig. 4.

fascicular xylem\* for the secondary wood opposite the ends and on the flanks of the primary xylem respectively; the former is distinguished by its later development and by the much smaller diameter of the tracheids, a characteristic feature also of the genus *Sphenophyllum*.

The secondary tracheids of the interfascicular wood frequently bear three rows of bordered pits on the radial walls and considerably exceed in breadth the elements of the stem-wood. The radial breadth of the root-elements formed during the first year's growth in thickness is approximately  $60\mu$ , and in a tangential direction  $38\mu$ ; tracheids of older secondary wood were found to be about  $38\mu$  wide between the tangential walls and between the radial walls  $33\mu$ . In the stem the corresponding measurements were approximately  $35\mu$  and  $28\mu$ . In addition to the fairly conspicuous medullary rays of normal form, single parenchymatous cells frequently occur among the tracheids, reminding one of the medullary-ray elements in *Sphenophyllum plurifoliatum*.†

The secondary wood of the root exhibits more or less distinct indications of rings of growth, and the late summer tracheids occasionally have bordered pits on their tangential walls.

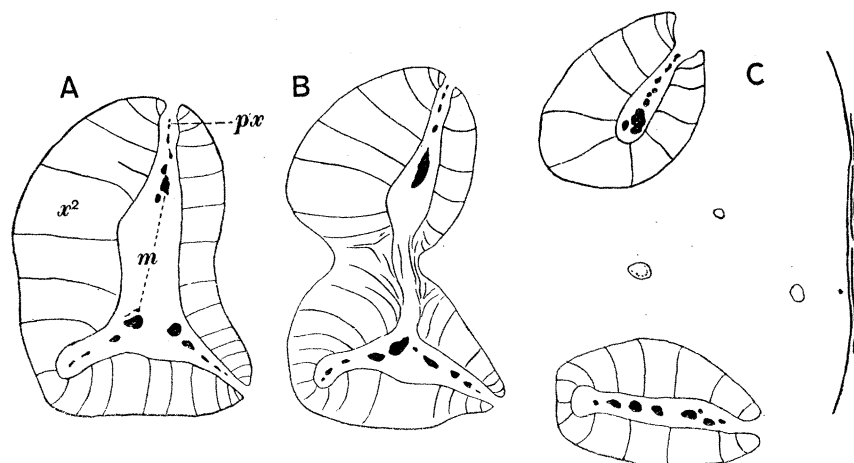


FIG. 19.—*Araucaria Bidwillii*. Branching root-stele.

The most interesting feature observed in the roots of *Araucaria Bidwillii* is illustrated by the diagrammatic drawings, fig. 19. Fig. 19, A, represents the stele of a comparatively young root from which the cortex has been exfoliated; the longest diameter of the pericycle is 6 millims.; the metaxylem (*m*) consists of detached groups of tracheids surrounded by conjunctive parenchyma, and the protoxylem is represented by crushed and almost obliterated elements at the three angles of the stele. The fascicular xylem has been formed across one angle only. At a slightly higher level the stele is seen to be constricted in the middle (fig. 13, B)

\* WILLIAMSON and SCOTT (1894), p. 924.

† *Ibid.*, Plate 75.

where the secondary tracheids are cut across in an obliquely longitudinal direction, passing left and right to the two halves of the dividing stele. The next stage is shown in fig. 19, c; the pericycle, the edge of which is shown by the line to the right of the drawing, has now reached a diameter of 8 millims., encloses two distinct steles. These reunite at a higher level and the stele resumes its normal appearance. This unusual phenomenon suggests a comparison with the dichotomous branching of certain lycopodiaceous roots, but we are doubtful as to its morphological significance.

*Araucaria imbricata*.—The young roots have a diarch stele and a pericycle about eight cells in breadth with several (frequently eight) canals arranged symmetrically in a ring. At a later stage the metaxylem occurs as scattered groups of tracheides and the development of the secondary xylem follows the course already described in the case of *A. Bidwillii*. The endodermis is a well-marked layer with suberised radial walls; the suberisation extends to the next cortical layer and occurs spasmodically on the walls of the third layer. The secondary xylem exhibits the usual root characteristics, namely, thinner walls and larger lumina than in the stem elements. The development of the lateral roots has been described by VAN TIEGHEM and DOULIOT\* in *Araucaria brasiliensis* and *A. excelsa*.

## VII. LEAVES.

a. *Agathis*.†—Reference has already been made in a former section of this paper to the form and size of the leaves in the several species. The lamina is traversed by several parallel veins (about 16 in the widest part of the leaf in *Agathis australis* and in the broader leaves of the other species considerably more) which bifurcate as they diverge from the narrow base traversing the lamina as single veins, usually without further dichotomy, and dying out against the margin of the lamina as it becomes gradually narrower towards the apex. The drawings reproduced in fig. 20, A, illustrate the venation characteristic of an *Agathis* leaf.

The secretory canals (omitted in fig. 20, A) are clearly seen as transparent lines between the veins of a leaf from which the chlorophyll has been removed.

We have examined the anatomy of the following species:—*Agathis australis*, *A. loranthifolia*, *A. robusta*, *A. obtusa*, *A. vitiensis*, and *A. Moorei*. In essentials the leaves of the various species exhibit but slight differences; the variations in the amount of palisade tissue and the abundance, or almost complete absence, of thick-walled fibres and branched idioblasts is probably rather an expression of differences in environment than a trustworthy index of specific types. The most striking generic characters are the alternation, in a horizontal plane, of secretory canals and vascular bundles and the occurrence of large and curiously branched idioblasts in the mesophyll.

\* VAN TIEGHEM and DOULIOT (1888), p. 348, fig. 379.

† For references to the structure of the leaves of *Agathis* see THOMAS (1865), in addition to the papers cited below.

The comparatively thick and stiff leaves of *Agathis australis* and *A. obtusa* have a thicker cuticle and greater abundance of hypodermal fibres and branched idioblasts than the thinner leaves of the other species. The stomata of all the species conform to one type; the guard-cells are situated on the floor of a cup-like depression with a projecting thick-walled rim as described by MAHLERT,\* HILDEBRAND,† and BERNARD.‡ Thick fibres occur more or less abundantly below the upper epidermis and, to a less extent, next the lower epidermis. The mesophyll usually exhibits a well-marked differentiation into palisade and spongy parenchyma, but in *A. loranthifolia* and *A. vitiensis*, at least in such leaves as we have seen, the palisade tissue is either feebly developed or absent. In the leaves of *A. obtusa* the cells of the mesophyll next the lower epidermis form a palisade layer of shorter cells than those below the upper epidermis, but as a rule the lamina exhibits the normal dorsiventral structure. The mesophyll of *Agathis australis* possesses an abundance of large thick-walled idioblasts with the walls of their numerous arms thickly set with small crystals. Precisely similar elements occur in the leaves of other species, but in some of the thinner and softer leaves they are much less numerous, and in *A. vitiensis* they appear to be particularly scarce. BERTRAND§ states that *A. loranthifolia* is distinguished by the absence of these sclerites; but in leaves referred to this species, which we have examined, several sclerites were observed. There can be little doubt that these cells serve to bind together the loose tissue below the palisade layer, and as HABERLANDT suggests, such thick-walled elements may be compared with the grains of sand in mortar or the glass powder which is used to reduce the compressibility of guttapercha.||

The long arms of the sclerites extend through the open tissue of the lamina and are often seen to be bent in such manner as to lie against the wall of a mesophyll cell. Their irregular shape probably renders them more efficient as clamping cells in the spongy leaf-tissue than if they had the form of ordinary fibres; the fact that these elements are less branched and more like normal parenchymatous cells in the firmer and less open tissue of the leaf base would seem to favour this view.

The vascular bundles are accompanied above and below by a few fibres and by secretory cells; in *Agathis obtusa* these cells are larger and thicker than in other species; additional strength is occasionally afforded in the case of the stiff leaves of this species by a palisade cell becoming lignified and functioning as a mechanical element as in the familiar *Hakea* leaf. There appears to be no well-defined sheath of large clear cells such as usually surrounds the vascular bundles of leaves. In several instances we have noticed centripetal xylem elements above the

\* MAHLERT (1885), fig. 14.

† HILDEBRAND (1860), Plate 4.

‡ BERNARD (1904), Plate 3.

§ BERTRAND (1874), p. 119.

|| HABERLANDT (1896), p. 141.

protoxylem, and a few reticulate transfusion tracheids usually occur on the flanks of the xylem.

The transfusion tracheids do not constitute a prominent feature in *Agathis* leaves as they do in *Araucaria*. BERNARD\* has investigated in detail the structure and distribution of these elements, which he speaks of as centripetal xylem; he states that in the basal portion of the lamina they are few in number and confined to the sides of the centrifugal xylem; farther up the lamina they tend to form an arch and thus convert the endarch into a mesarch bundle, ultimately increasing in number until the centrifugal elements die out and in the apical region the veins are represented solely by centripetal tracheids. The transfusion tracheids, as seen in longitudinal section, appear to be identical in structure with the short and broad tracheids described by HEINRICHER† as storage tracheids in species of *Centaurea* and other leaves, elements which he regards as modified cells of the bundle-sheath. The transfusion cells of *Agathis* have exactly the same form as the accompanying mesophyll cells, from which they may be derived, and differ considerably in size from the normal tracheids.

#### b. *Araucaria*.

We have already noticed some of the external features of the leaves under the brief descriptions of the several species. The flatter leaves of the *Colymbea* species, with their numerous veins alternating with resin-canals, are readily distinguished from the narrower leaves of the *Eutacta* section of the genus, which are characterised by a more or less tetragonal or elliptical section, and by the resin-canals being scattered through the mesophyll, with no constant relation to the vascular bundles, or occurring below each vein (*A. Rulei*); in the leaves of tetragonal section one canal frequently traverses the tissue at each angle. In all the species examined, thick-walled idioblasts (fig. 20, F) are met with in the mesophyll; in the softer and more delicate leaves of *A. brasiliensis* these elements appear to be scarce, but in the other leaves they are abundant, especially in *A. Rulei*, where they attain considerable size.

Professor BERTRAND‡ has published a "Tableau synoptique des caractères anatomiques des espèces du genre *Araucaria*," based on the position of the resin-canals, on the number of veins and on the number of rows and distribution of the stomata. Our investigations have convinced us that all these diagnostic characters are untrustworthy and far from constant. The veins vary in number in the leaves of a species according to the part of the lamina examined and the age of the leaf. The rows of stomata exhibit similar variations; for example, *A. imbricata*, said by BERTRAND to have 70 rows, may have any number from

\* BERNARD (1904), pp. 292-297, figs. 62-73. See also WORSDELL (1895), p. 313, fig. 20.

† HEINRICHER (1885), Plate 1.

‡ BERTRAND (1874), p. 117.

60 to 80. The statement that the *Eutacta* species are characterised by canals below the bundles does not hold good; in fact, with the exception of *A. Rulei*, the canals are seldom met with under the veins.

A noteworthy characteristic of the genus is the rich development of transfusion tracheids (centripetal xylem); as this tissue has already been described by more than one author, we do not propose to deal with it in detail. Reference may be made to the papers of WORSDELL and BERNARD,\* and especially to the figures published by the latter.

All the species possess stomata situated on the floor of fairly large pits.† Owing to the abundance of wax in the stomatal depressions, the arrangement of the stomata in irregular and occasionally discontinuous rows is clearly seen by examining dry leaves under a lens. In *Araucaria imbricata* stomata are abundant on both faces of the lamina; they occur on both surfaces also in *A. brasiliensis*, but in *A. Bidwillii* the upper epidermis contains so few that it may be said to be practically destitute of stomata. In *A. Rulei* (fig. 20, B-D) we have an example of a leaf in which the stomata (represented in the figure by rows of dots) are confined to the upper epidermis (B), with the exception of a few short rows at the base of the lower surfaces (C). The falcate form of the leaf of the broad base is shown in fig. 20, D. In the other *Eutacta* species stomata usually occur over the whole of the epidermis.

Sect.: COLYMBEA. *Araucaria imbricata*.—The cotyledons exhibit a well-defined differentiation into palisade and spongy parenchyma. Hypodermal fibres occur below the upper and under epidermis. The vascular bundles are usually accompanied by fairly abundant transfusion-tracheids in a form of a conspicuous arc above the centrifugal xylem. The resin-canals alternate with the veins, but occasionally a canal is seen underneath a vascular bundle. The leaves of the seedling differ from those on the older shoots chiefly in their softer texture, due to the comparatively feeble development of mechanical elements. We noticed that the transfusion tracheids in the apical region of a young leaf constituted nearly the whole of the xylem, a fact in accordance with BERNARD's description of this tissue in the leaves of *Agathis*.

The mature type of leaf is characterised by numerous short and broad ribs of hypodermal fibres below the upper epidermis comparable to those in leaves of *Cordaites*. The mesophyll in some leaves is almost uniform in structure, while in others it exhibits a differentiation into palisade and loose parenchyma, the former tissue being represented on both faces. Contrary to BERTRAND's statement,‡ numerous large and lignified idioblasts are scattered through the mesophyll. The mesophyll in this and other species contains a considerable number of thin-walled and clear cells which probably serve as water reservoirs. The vascular bundles are

\* WORSDELL (1895); BERNARD (1904).

† For figures and descriptions of stomata see HILDEBRAND (1860), p. 149; STRASBURGER (1866), Plate 42; MAHLERT (1885); THOMAS (1865).

‡ BERTRAND (1874).



characterised by an exceptionally large number of centripetal tracheids\*—broad and short elements with numerous circular pits in their walls—and this tissue is especially well developed where a bundle ends blindly in the lamina; each bundle is surrounded by a layer of large parenchymatous cells which may contain tannin. The thinner and softer leaves of *Araucaria brasiliensis* differ from those of *A. imbricata* in the much feeble development of hypodermal fibres and scattered idioblasts, as also in the thinner cuticle and smaller number of stomata on the upper surface.

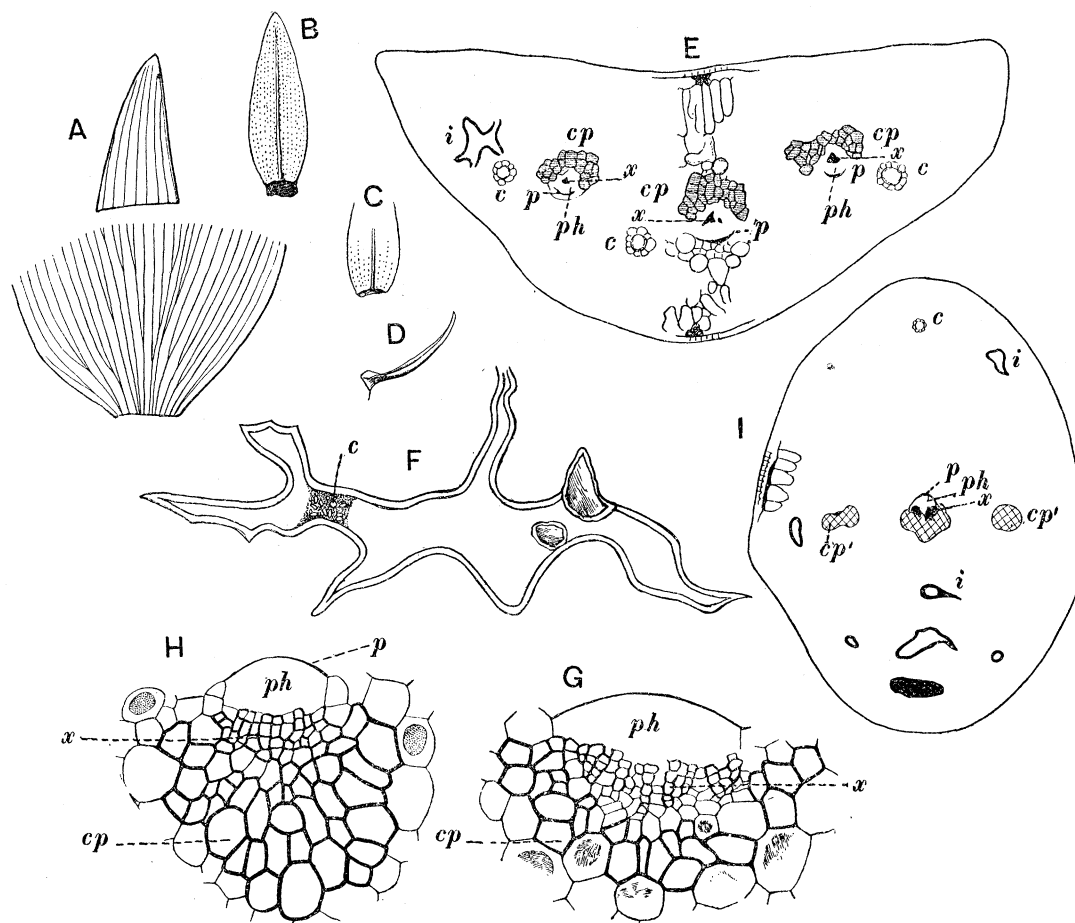


FIG. 20.—A, *Agathis* leaf; B-D, F-H, *Araucaria Ruleri*; E, *A. brasiliensis*; I, *A. Balansee*.

The lamina is differentiated into palisade and spongy tissue, the former being present also, though to a less extent, next the lower epidermis. Several bundles occupy the median plane alternating with secretory canals. A few idioblasts (fig. 20, E, *i*) occur scattered through the loose mesophyll. In the diagrams represented in fig. 20, E, I, G, H, the phloem region is left blank (*ph*), but the position of the protophloem is shown at *p*. As we pass from the base towards the apical portion of the lamina, the amount of centripetal xylem (*cp*. fig. 20, E) gradually increases at the expense of the centrifugal elements, *x*, and close to the

\* BERNARD (1904), fig. 88, p. 305.

apex (fig. 20, E) the structure of the lamina conforms very closely to that of the *Eutacta* leaves, showing that there are no well-defined features distinguishing the leaf-anatomy in the two groups of species. WORSDELL\* has described the transfusion tracheids in the cotyledons and in the adult leaves of *Araucaria Bidwillii*. Branched sclerites are abundant; the centripetal xylem is similar to that of *A. imbricata* and, as in other species, it decreases in amount towards the base of the lamina.

Sect. : EUTACTA. *Araucaria excelsa*.†—The larger leaves of this species, such as occur on the main stem, are richly provided with secretory canals. Branched sclerites are distributed through the mesophyll as in other species of the genus; hypodermal fibres, palisade tissue, and stomata occur on both the upper and lower surface of the broadly oval lamina. The mesophyll cells are elongated at right angles to the leaf-surface, except in the median plane, where they tend to form horizontal connecting cells between the bundles of which there may be six or more. The smaller tetragonal leaves of young shoots are almost destitute of hypodermal fibres and usually have four resin-canals, one at each corner, and a single median vein. In the basal portion of the leaves of *Araucaria Cunninghamii* we found three vascular strands, a central one of normal structure and two lateral bundles consisting solely of transfusion tracheids; these accessory strands, which do not extend far up the lamina, no doubt represent remnants of ordinary leaf-veins. The mesophyll contains numerous canals and idioblasts. *Araucaria Cookii*‡ is characterised by broader leaves with several vascular bundles. In all the *Eutacta* species we have examined, centripetal xylem forms a conspicuous feature.

*Araucaria Rulei*.—The leaves of this species are peculiar in having the stomata practically confined to the upper surface. They are bent upwards from the axis at an angle of about 45° (fig. 20, D) and the apical part is turned inwards; this position and the close spiral in which the leaves are disposed render the lower surface the more exposed, and it is no doubt for this reason that the morphologically upper surface exhibits all the structural characters of a lower surface. The cuticle is unusually thick, especially on the lower epidermis; the lower hypoderm is well developed, but the fibres do not project into the mesophyll in the form of blunt ridges as in *A. imbricata*. The palisade tissue is also much better developed in the lower half of the lamina. The bundles have a large amount of centripetal xylem, which in the apical region of the leaf (fig. 20, H, *cp.*) constitutes the greater part of the veins; in the basal portion of the lamina (fig. 20, C) this tissue is still abundant, but to a less extent than near the apex. The elements of the centripetal xylem exhibit a more definitely reticulate structure than would be inferred from BERNARD's figures. In *A. Rulei* a resin-canal occurs below each vein, and in the base of the

\* WORSDELL (1895).

† For a description of the cotyledons see WORSDELL (1895), Plate 26, fig. 17.

‡ BERNARD (1904), fig. 87, p. 304.

lamina these secretory canals have a very large diameter. The abundant, thick-walled sclerites reach an unusual size (fig. 20, F). *A. Rulei* constitutes a well-marked type; it is pre-eminently xerophytic in structure; in its flatter shape, and in the larger number of bundles it constitutes in some measure a link between the leaves of the two sections of the genus.

*Araucaria Balansa*.—A section of the small, falcate, and laterally compressed leaf of this species presents the form of a four-sided, lozenge-shaped figure with rounded angles (fig. 20, I). The single bundle, which traverses the mesophyll slightly below the middle, consists of a few short rows of narrow centrifugal tracheids, *x*, and a considerable development of large centripetal elements, *cp*. On each side of the median vein there is a smaller vascular bundle mainly or wholly composed of centripetal tracheids, *cp'*; these lateral strands gradually die out in their course through the lamina, terminating in a few centripetal or transfusion tracheids. The epidermis, with its thick cuticle, is succeeded by a layer of hypoderm fibres, and the mesophyll next the epidermis has the form of short palisade cells; the greater part of the mesophyll consists of loose parenchymatous cells elongated in a direction parallel to the long axis of the leaf-section. Thick-walled, branched idioblasts encrusted with calcium oxalate crystals are fairly abundant, and a single canal runs through the lamina close to the lower angle.

#### VIII. LEAF-TRACES.

As the course of the leaf-traces in species of *Agathis* and *Araucaria* has already formed the subject of an investigation by GEYLER,\* we do not propose to traverse in detail the same ground. A single leaf-trace bundle is given off from the stem; this breaks up in its passage through the cortex into three, or sometimes into a large and small strand, the larger dividing into two—each leaf-base receives therefore three vascular bundles, and these may undergo further branching in the lamina.

In a paper published in 'Flora' in 1885, MARKFELDT† deals with the interesting question of the behaviour of leaf-traces during the increase in thickness of a stem or branch.

Sir WILLIAM THISELTON-DYER‡ has drawn attention to the ease with which persistent leaf-traces may be seen with the naked eye on a tangential surface of Araucarian wood. In a photograph of *Araucaria imbricata* which he figures, the spirally-disposed traces are shown with remarkable distinctness; the question raised as to whether the leaf-traces are prolonged indefinitely may, we believe, be answered in the affirmative.

\* GEYLER (1867).

† MARKFELDT (1885).

‡ THISELTON-DYER (1901), p. 423, Plate 22, fig. 3.

This is one of the many problems on plant-anatomy on which one vainly refers to text-books for information. The question is, what happens to a leaf-trace as each annual zone of wood is formed by the cambium in trees which retain their leaves more than one year?

Among other species, MARKFELDT deals with the leaf-traces of *Araucaria brasiliensis*, a species in which the traces follow an oblique course through the secondary wood. In a branch two years old, the spiral elements adapt themselves by stretching to the increased distance between the inner edge of the stem wood and the cortex; towards the end of the second year some of them begin to tear, and in the third year tearing occurs on a larger scale. As the rupture occurs in the cambial zone and the upper elements break first, a gap is formed. The cambium then produces new xylem tracheids which are added to the lower edge of the trace, the gap formed by the tearing of the upper trace elements remains, and in each succeeding year, so long as the continuity of the trace is maintained, the tearing of the tracheids produces a step-like gap in the obliquely ascending leaf-trace.

MARKFELDT describes an interesting case in *Araucaria* in which he found that the cambium of the stem continued to add new elements to the trace long after leaf-fall. A further contribution to this subject was made by TISON\* in 1903, in which the behaviour of Gymnosperm leaf-traces is treated with greater fulness. Before the rupture of the uppermost (oldest) elements of the trace, which occurs, as MARKFELDT said, in the cambial region, new tracheids have already been produced by the stem-meristem, and these are in continuity with the tracheids of the cortical portion of the leaf-trace at one end and at the other they abut on the elements of the stem-wood. The newly-formed elements are spiral or reticulate. TISON notes that the rupture of the tracheids takes place gradually during the year; he did not observe the successive step-like gaps observed by the German author. A tangential section of the stem-wood in the region of a leaf-trace shows thick-walled, medullary-ray cells lying above tracheids which decrease in diameter from below upwards.

The leaf-traces of *Agathis obtusa* described by TISON pursue an almost vertical course through the cortex; the numerous strands from the leaf-lamina fuse in pairs and are finally reduced to two bundles which enter the stem cylinder 6-7 centims. below the level of the leaf-insertion. The branches examined were not more than five years old, and in these no actual rupture of the elements was observed nor were any new elements ("tissus de raccard") added. The fact that no break occurs in this species during four to five years is, as TISON says, due to the obliquely vertical course of the trace as it passes through the wood, a circumstance which means that the increasing diameter of the stem exerts a pressure which is lateral rather than vertical.

\* TISON (1903).

In *Araucaria imbricata* and *A. brasiliensis* the traces are also oblique in their course, but less so than in *Agathis obtusa*. TISON speaks of *Araucaria* as exhibiting an unusual persistence of the leaf-trace elements, a fact previously noticed by MARKFELDT. The French author mentions a stem of *Araucaria brasiliensis* with 25 annual rings in which the leaf-traces were intact. Sir WILLIAM THISELTON-DYER\* has described persistent traces in a stem of *A. imbricata* with 60 rings of growth, and it would seem highly probable that in *Araucaria* the traces may prolong their existence indefinitely.

We have examined the leaf-traces *Araucaria imbricata*, *A. brasiliensis*, *A. excelsa* and *Agathis robusta*. The tracheids formed during the first year contain not only spiral and annular elements as stated by MARKFELDT, but also tracheids with bordered pits.† Plate 24, fig. 21, A, represents a leaf-trace of *A. imbricata* as seen in a radial longitudinal section of a branch two to three years old. A strand of thick-walled (pericycle) fibres is seen at *f*, the xylem of the trace consists at the inner edge, *a*, of a tangle of delicate spirals succeeded by tracheids with their longitudinal walls intact and the spiral band less extended; the outer elements possess small oval pits. The cambium cells as the trace enters the secondary wood curve obliquely downwards and abut on the ends of the tracheids at *c* and at this region, as described by TISON,‡ new elements are added to the xylem of the trace. The tissue *d* between the upper edge of the trace and the secondary wood of the stem, *e*, consists of unligified parenchyma. The irregular and broken upper edge of the trace, *g*, is due to the wrinkling and bending of the partially disorganised spiral tracheids. Fig. 21 B shows a section through a leaf-trace of an old stem. A portion of the trace seen in the secondary wood consists of horizontal tracheids in different stages of stretching and tearing and below these of tracheids bending inwards and downwards into continuity with the stem wood; above the xylem at *a* occur parenchymatous elements and numerous stone-cells. The portion of the trace shown in the cortex has been torn and disorganised, and thus continuity is no longer maintained.

It is often difficult to distinguish between a broken leaf-trace in the cortex and an apparent break in the vascular strand due to a sudden bending of the trace near the outer edge of the secondary wood.

Fig. 21, c, illustrates the steeper course through the secondary wood of a leaf-trace of *Agathis robusta* (two to three years old). The inner and upper edge of the trace consists of tangled and extended spiral bands and above these occur parenchymatous elements and pitted stone-cells: the lower tracheids of the trace show bordered pits on their walls. The lighter patches *a*, interrupting the continuity of the xylem of the trace, appear to be due to tearing of the oldest and uppermost tracheids.

Fig. 21, d, shows the appearance presented by a leaf trace of *Araucaria imbricata*

\* THISELTON-DYER (1901).

† Cf. TISON (1903), Plate 3, fig. 18.

‡ TISON (1903), p. 65, Plate 2, fig. 2.

as seen in a tangential section of wood 50 years old. The trace consists in the lower part of rows of tracheids succeeded by a larger group of thick-walled elements or stone-cells. Some of the tracheids of the stem wood, *x*, exhibit very clearly spirally wound lines representing small channels containing air which have been eaten out of the tracheid walls.

Both *Araucaria* and *Agathis* possess leaf-traces composed of both spiral tracheids and tracheids with oval and circular bordered pits; in the latter genus the traces pursue a steeper course through the wood than in *Araucaria*; in both genera the medullary ray tissue lying above the trace in its course through the secondary wood consists largely of thick-walled elements. Another feature worthy of note is the occurrence of a few short tracheids lying in the parenchymatous tissue of the pith of the branch which fills the foliar gap formed by the bending outwards of the trace.

In a transverse section of the wood of *Araucaria* a leaf-trace is sometimes seen passing in a horizontal direction through a medullary ray; the tracheids with slender spiral bands which form a considerable proportion of the trace bear a close resemblance to the spirally thickened elements in the medullary rays of a *Lepidodendron* stem.

#### IX. REPRODUCTIVE SHOOTS.

A noticeable feature in the male and female strobili of the Araucarieæ, more particularly of the genus *Araucaria*, is the gradual passage between foliage leaves and sporophylls. The transitional stages are particularly well seen in the female cones of *Araucaria imbricata* and *A. Rulei* (fig. 22, A); in the cones of some of the other species (*e.g.*, *A. Cookii*) the transitional stages are more or less obscured by the bending down of the lower cone-scales and the consequent hiding of the intermediate appendages which occur at the base of the cones. In the female cone of *Pinus* and other genera of the Abietineæ the cone-scales are much more clearly differentiated from the foliage leaves and follow them with greater abruptness. In the male flowers of *Araucaria* a transition may also be traced between foliage leaves and sporophylls, and in this case no one doubts the homology. The equally striking transition between the scales of the female cone and foliage leaves does not receive an equally simple interpretation at the hands of many botanists. If the cone-scale of *Araucaria* and *Agathis* is not to be regarded as a leaf, differing only in certain distinctive characters assumed for a special purpose, it affords a striking instance of the difficulty of recognising true morphology owing to extreme modification "resulting from certain special adaptive requirements."\* We prefer to accept the simpler interpretation of the cone-scale with its ligular outgrowth as a leaf modified for the purpose of bearing an ovule.

So much has been written on the morphology of the female shoots of the Coniferales that an attempt to give a general summary of the views and arguments advanced

\* WORSDELL (1904), p. 57

would extend the limits of our paper beyond reasonable bounds. Mr. WORSDELL'S contribution to the "Annals of Botany" on this subject constitutes a comprehensive and exceedingly useful digest of the growth of the several views and of the facts on which they are based.\*

The main question with which we are concerned is this: considering the cones of the Araucarieæ *per se*, what interpretation of their structure is most in accordance with facts; are we to regard them as practically inseparable from the cones of the Abietineæ from the point of view of morphology, or may we consider them on their merits as representing a type which may or may not fall into line with other forms of female shoots met with among Conifers?

We prefer to consider the cones of *Agathis* and *Araucaria* as types to be interpreted apart from such considerations as have been founded on the structure of the more complex type represented by *Pinus* or *Abies*. This preference is based on the following considerations:—

The Araucarieæ are, we believe, older than the Abietineæ and in many respects they afford what we consider satisfactory evidence in favour of the view that they constitute a more primitive branch of the Gymnosperms. It is the Abietineous cone which has chiefly exercised the ingenuity of morphologists; after coming to a decision as to the most probable interpretation of this comparatively modern and highly specialised type, the next step would seem to be the application of the same interpretation to the cones of other families of Coniferæ. If we decide to style a pine-cone an inflorescence—the expression of a theory which we do not propose to discuss—we are almost driven by the example of botanists who have dealt with this subject to apply the same description to the cones of the Araucarieæ. We do not presume to deny that the various forms of cones may be constructed on one plan, in some of which the methods of construction are comparatively obvious, whereas others have almost completely lost those features which may serve as a guide to their morphology: but we venture to protest against a dangerous tendency to apply the methods employed in the case of the more recent and more highly specialised type to the older and less complex types. Roughly speaking, there are two alternatives to be considered: (*a*) the cone-scales of *Agathis* and *Araucaria* are essentially comparable with the cone-scales of the Abietineæ, and are to be regarded as being made up of a subtending bract and an axillary shoot,—structures of a twofold origin which have assumed an apparently simple form (*Agathis*) or have retained more or less obvious traces (*Araucaria*) of their double nature; (*b*) the cone-scales of the Araucarieæ are simple structures homologous with leaves which may, or may not, be homologous with the double cone-scales of the Abietineæ.

We believe that the second alternative is the more probable; but we do not commit ourselves to a definite expression of opinion in regard to the application of the same simple explanation to the structure of the Abietineous cone.

\* WORSDELL (1904).

A. *Male Flowers.*

The male flowers of the genus *Araucaria* differ from those of other members of the Coniferales in their much larger size (*cf.* figs. 8, B; 11, D, E; 13, A); their appearance is much more like that of the female cones than is the case in other genera and there is a less striking difference between the two kinds of reproductive shoots than is usually met with among Conifers. This closer agreement may, perhaps, be reckoned among the list of primitive characters.

In view of Dr. THIBOUT'S\* work "Sur l'appareil mâle des Gymnospermes," it is unnecessary to describe in detail the results of our own investigations, but the following summary includes species which are not dealt with by the French author.

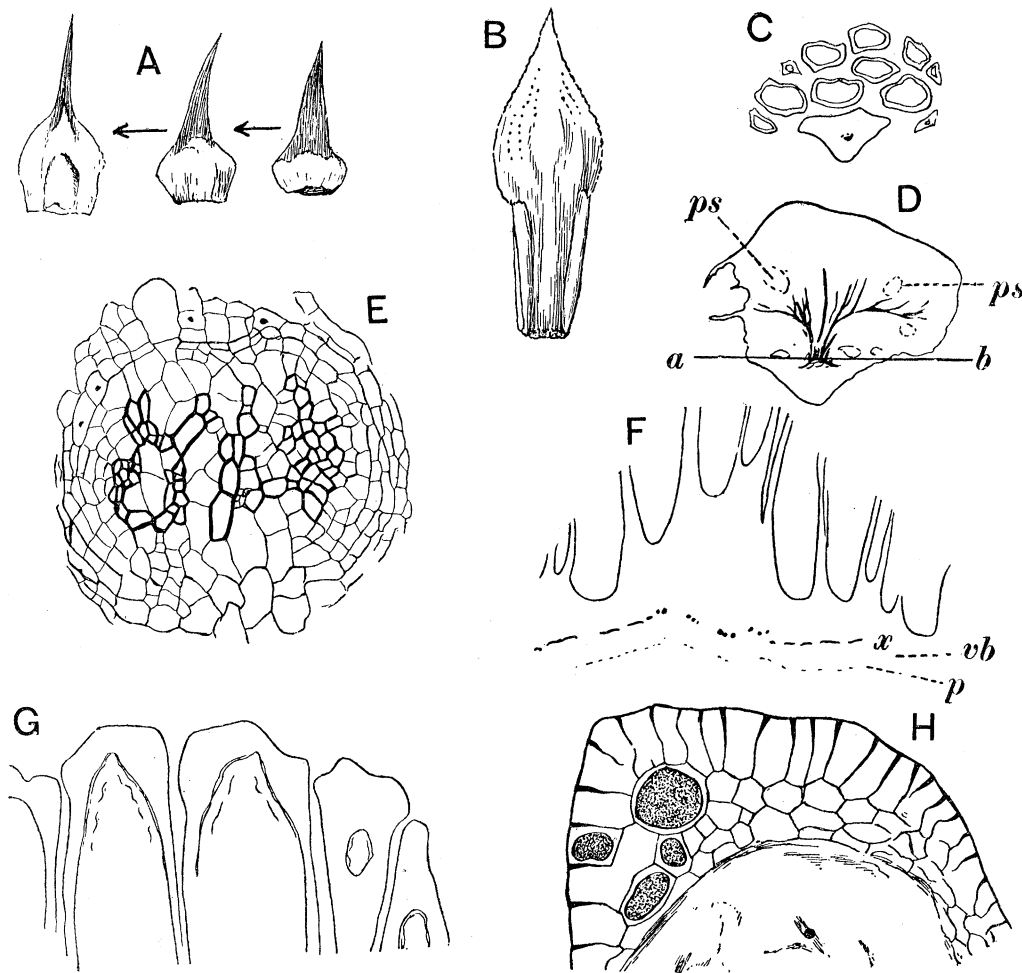


FIG. 22.—*Araucaria Rulei*.

*A. Rulei*.—The male flowers of this species (fig. 13, A), which attain a considerable length, differ from those of *A. imbricata* in their longer and narrower form. The sporophylls, approximately 1 centim. long, are characterised by a lanceolate, distal

\* THIBOUT (1896).



termination slightly oblique to the pedicel and not sharply bent upwards as in *A. imbricata*; a few rows of stomata occur on the upper surface of the lamina (fig. 22, B) and a smaller number are scattered over the lower face. The sporophylls which we examined bore 11 pollen-sacs (fig. 22, c). A single, collateral, vascular bundle enters the pedicel, this soon divides into two, and occasionally a third and smaller strand is given off. The two bundles bend slightly towards one another so that the two groups of xylem present the appearance of a broadly open V. This pair of vascular strands gives off a fairly large branch at right angles to the pedicel, which soon bifurcates and, as the two arms spread upwards and outwards, several smaller branches pass to the bases of the pollen-sacs (fig. 22, D), some of which have been shaved across (*ps.*) in the section. If a tangential longitudinal section is cut along the line *ab* in fig. 22, D, the bifurcating bundle appears to have a concentric structure (fig. 22, E), but in reality it consists of two contiguous collateral strands. Fig. 22, F, represents another longitudinal tangential section in which the bases of several pollen-sacs are seen embedded in the tissue of the sporophyll and below the sacs the small vascular bundles *vb.* are cut across in a transverse and obliquely longitudinal direction. It would seem, then, that the vascular bundles do not penetrate into the microsporangia but terminate just below the point of insertion. The distal end of the same section (fig. 22, G) shows the blunt terminations of a few microsporangia, and the structure of the end wall of one of them is illustrated in fig. 22, H. The surface layer is characterised by thickening bands at right angles to the surface and the smaller-celled tissue between the surface and the tapetum is richly supplied with large secretory cells. The wall of the pollen-sacs is of the type described by THIBOUT in *Araucaria Cookii*. The appearance presented by the tangentially-cut long and narrow microsporangia arranged in two series bears a resemblance to that presented by sections of *Cheirostrobos*.<sup>\*</sup> The thickening bars on the superficial cells in the sporangia of *Cheirostrobos* appear to be identical with those in *Araucaria*: it is worth noting that the tracheæ in the interior of the stele of the fossil possess multiseriate bordered pits.<sup>†</sup> The ground tissue of the sporophyll contains numerous sclerites and the distal lamina with its single vascular strand is protected by a thick cuticle.

*Araucaria imbricata*.—The large oval male flowers of this species bear numerous sporophylls consisting of a pedicel bending up at right angles beyond the microsporangia into a triangular, acuminate lamina (fig. 23). The horizontal portion of the sporophyll (A, B) is 1.9 centim. long. A single bundle enters the pedicel; after becoming elongated tangentially into a comparatively narrow band it divides into two and may also give off a smaller accessory strand; the three bundles gradually separate from one another, and farther up the pedicel they may again divide into four or five bundles, which near the distal end of the sporophyll are accompanied by a considerable amount of large and stout centripetal xylem elements. The method of

<sup>\*</sup> SCOTT (1897), Plate 2, figs. 9 and 10; Plate 5, fig. 12.

<sup>†</sup> *Ibid.*, Plate 5, fig. 13; Plate 5, fig. 16; and Plate 6, figs. 22, 23.

branching to supply the microsporangia agrees with that in *A. Rulei*. The microsporangia, 19 in number in the example shown in fig. 23, c, are arranged in two series and agree structurally with those of *A. Rulei*. The pollen-grains are spherical and possess a cuticularised exine and a very thick inner membrane of cellulose.\*

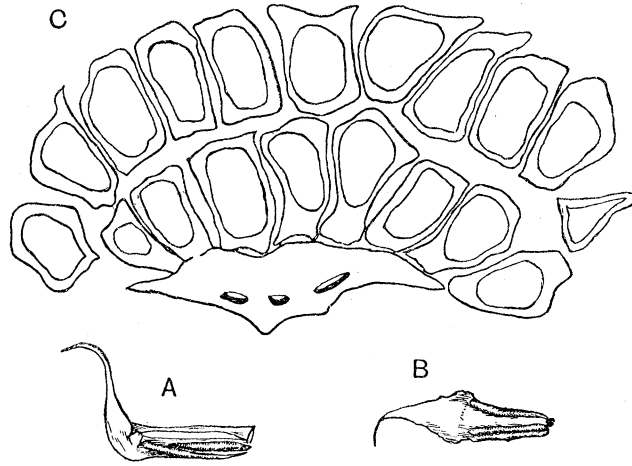


FIG. 23.—*Araucaria imbricata*.

In *A. imbricata* the thickening bands of the superficial layer of the microsporangia are particularly numerous and conspicuous. The male flowers of *Agathis* differ from those of *Araucaria* in their much smaller size and in the bluntly-rounded distal termination.† In *Agathis australis* there are only three pollen-sacs supplied by branches from the single vascular strand of the pedicel; the epidermal layer exhibits the characteristic thickening bands, and the general structure is similar to that of *Araucaria*.

#### B. Female Flowers.

The external form and dimensions of the cones of the several species of *Araucaria* and *Agathis* have already been described. Before proceeding to deal with anatomical characters we may briefly consider the features exhibited by the cone-scales in both *Agathis* and *Araucaria*.

*Agathis*.—The female flowers of the several species conform to a uniform plan and such differences as may be detected between one species and another are too insignificant to call for special treatment.‡ The cone of *Agathis Moorei* represented in fig. 1, A, agrees fairly closely with those of the majority of the species. It is almost spherical (11 centims.  $\times$  10 centims.); the smooth surface formed of the imbricate and interlocking ends of the scales recalls that of the cones of *Cedrus*, and as in the cedar the scales at the apex adhere together after the fall of the others. A single scale has a length of 3.7 centims., and at the widest part measures

\* LOPRIORE (1905).

† Cf. THIBOUT (1896), Plate 10, fig. 18 (*A. robusta*).

‡ Material received from Professor TREUB, which is now under investigation, may throw further light on the morphology of the female flowers of *Agathis*.

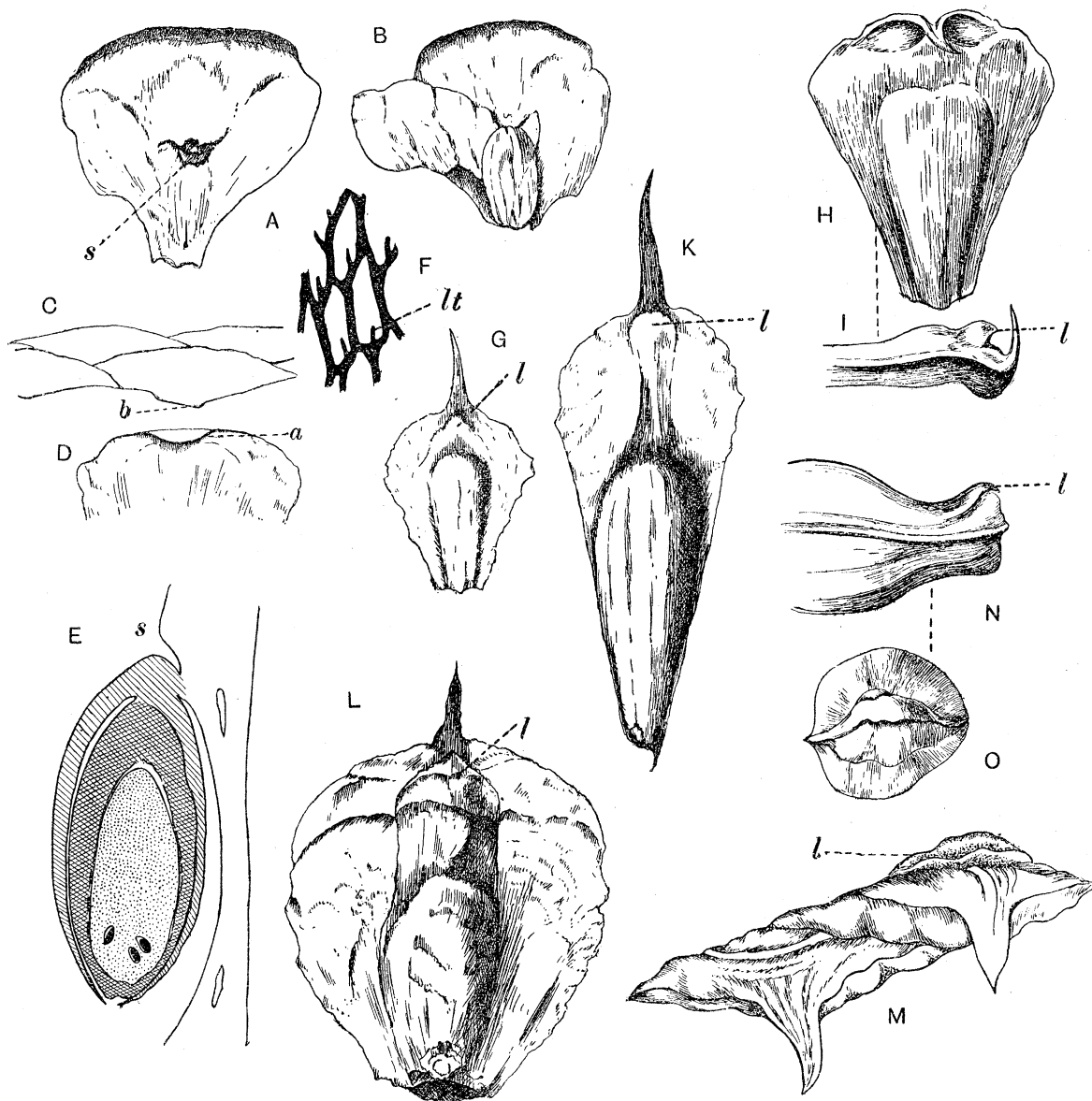


FIG. 24.—A-D, *Agathis Moorei*; E, *A. loranthifolia*; F, *A. vitiensis*; G, *Araucaria Cookii*; H, I, *A. excelsa*; K, *A. imbricata*; L, M, *A. Bidwillii*; N, O, *A. brasiliensis*.

3·3 centims. in breadth; it is broadly triangular with a thin truncate base supplied by a single vascular bundle. The seed lies in the middle line; the large wing projects beyond the edge of the scale (24, B), and rests on the surface of the adjoining cone-scale. The edges of the scale are thin and membranous and asymmetrical. On removal of the seed the narrow attachment of the seed-base to the scale is shown by the scar (s, fig. 24, A). The narrow connection between seed and scale is shown also in fig. 24, E (*A. loranthifolia*), a diagrammatic sketch made from a photograph, for which we are indebted to Mr. THOMSON, of Toronto. In order to keep intact a dry and ripe cone of *Agathis* it is necessary to bind the scales

together; the suddenness with which the apparently solid and compact cone falls to pieces on loosening the wire or string with which it has been bound is very striking and worthy of a passing reference. An examination of the scales affords an explanation of this phenomenon. Looking at a scale from below one notices a fairly prominent ridge (fig. 24, D, *a*) at the edge of the scale and to one side of the median line. The margins of adjacent scales abut on the edge of this ridge, which acts as a check to the lateral shifting of the scales over one another; the edge of the curved ridge, *a* (fig. 24, D), is seen at *b* in fig. 24, C, which shows a few scales as seen on the cone-surface. Immediately the mutual pressure of the overlapping scales is disturbed their edges slip over the ridge, and the whole cone at once falls to pieces.

A portion of the vascular reticulum from the axis of a cone of *Agathis vitiensis*, shown in fig. 24, F, illustrates the manner of exit of the cone-scale bundles (*lt*) as single strands given off at a point slightly to one side of the lower angle of each mesh of the stelar network. The development of the ovule in *Agathis australis* has been described by DICKSON,\* and the same author refers briefly to the course of the vascular bundles. He regarded the scales of both *Araucaria* and *Agathis* as conformable morphologically to the Abietineous type. VAN TIEGHEM,† in 1869, gave a slight sketch of the course of the bundles in the cone-scale of this species, but the most complete account is that by STRASBURGER.‡ Our examination of the cone-scales of *Agathis vitiensis* is, in essentials, confirmatory of STRASBURGER's description of *A. australis*. A single bundle enters the base of the scale, and by repeated branching a series of 12 or more collateral vascular strands is produced. Eventually a bundle occupying a median position divides, and the strand turns on its axis until it occupies an inverted position above the lower series. This upper bundle then divides into two close to the base of the ovule, and subsequently an upper series of several strands is produced. The smaller number of inverted bundles described by STRASBURGER in *A. australis* is, doubtless, connected with the smaller size of the cone-scales. The characteristic features of a cone-scale of *Agathis* are:—(1) The absence of a definite outgrowth, or ligule, from the scale; the slight swelling immediately behind the base of the ovule (fig. 24, E, *s*) has been compared with the ligule of an Araucarian scale, but there is nothing which affords any clear indication of the double nature of the scale; (2) the single seed with a large wing on one side and a much smaller membrane on the other (fig. 24, B); (3) the continuance for a longer distance in the scale of a single series of bundles, before the few inverted bundles are given off, which supply the chalaza, as compared with the greater persistence of the double series in *Araucaria*.

*Araucaria*.—The cone-scales of the species of the Eutacta section of the genus, characterised by the thin lateral wings (figs. 24, H, I, G), and by the more prominent

\* DICKSON (1863, 1863<sup>2</sup>).

† VAN TIEGHEM (1869).

‡ STRASBURGER (1872).

ligule, are in marked contrast to the narrower and deeper scales of *A. imbricata* (fig. 24, K) without wings, and with a broader and more bluntly terminated ligule, *l*, which is free only at the apex and forms a much less conspicuous feature than in *A. Cookii* and other species of the *Eutacta* section. In the large scales of *A. Bidwillii*—a member of the *Colymbea* section—the scale has a considerable breadth, and the broad margins are thin and membranous (fig. 24, L, M). All the species have scales with a ligular outgrowth, *l*, and agree in having the ovule completely embedded in the tissues of the scale.

For the purpose of comparison, Araucarian cone-scales, as represented by *A. Rulei*, *A. excelsa*, *A. Cookii*, *A. imbricata*, *A. Bidwillii*, and *A. brasiliensis*, are shown in figs. 22, A, 24, G-O.

*Araucaria Rulei*.—At the base of a female flower the lowest cone-scales pass downwards by gradual transition into the foliage leaves (fig. 22, A); externally the chief distinguishing features of the former are: the division of the lamina into a broad basal portion and a long and narrow distal portion, the single median ovule and the subtending ligule terminating in a free broadly triangular apex with a fimbriate margin. The sterile leaf from the base of a cone shown in fig. 22, A (right), is practically identical with a foliage leaf, and has the same arrangement of vascular strands; this form is succeeded by a scale with a broader base traversed by a single row of vascular strands. The next stage in the transition is represented by a scale similar in external form but distinguished in section by the occurrence at one end of the scale of a vascular bundle with inverted orientation lying at a slightly higher level than the lower series of bundles; the same section shows also the beginning of the ligular outgrowth which has not yet become free, but consists of a low median ridge of tissue containing tannin-sacs. In the next stage a small, free appendage occurs to one side of the median line of the scale, and additional bundles are given off from the lower series, which become inverted and are confined to the more distal portion of the broad part of the scale.

The surface of the stout cone-axis, after removal of the scales, is characterised by spirally-disposed and contiguous rhomboidal depressions, from each of which a single bundle passes into the base of the scale. The micropyle which lies close to the proximal end of the scale has the form of a narrow and transversely elongated opening bounded by the integument.

The single vascular bundle before leaving the cone-axis gives off a strand (fig. 25, A, s) which turns through an angle of 180 degrees, and takes up the position shown in fig. 25, B. A section further from the base (fig. 25, c) shows five bundles below with an upper set of three. The bundles, especially those of the lower series, are accompanied by a few centripetal xylem elements. A layer of tannin-sacs forms the boundary between the small-celled tissue of the integument of the ovule and the lower part of the scale,\* in which thick-walled idioblasts

\* Cf. *A. Cookii*, as described by WORSDELL (1899), Plate 27, fig. 6.

abound. The nucellar tissue, *n*, is limited externally by a regular layer of cells similar to those which form the inner surface of the integument.

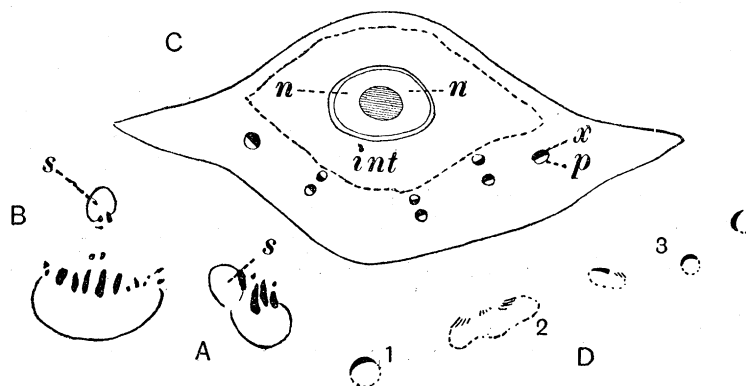


FIG. 25.—A–C, *Araucaria Rulei*; D, *A. imbricata*.

The bundle-system of *A. Rulei* is of the same type as that of *A. Cookii*. Fig. 26, A, represents a radial longitudinal section through a cone-scale (8 millims. long); portions of two vascular bundles are seen at *a* and *b*. The blunt apex of the long and narrow nucellus which projects through the micropyle consists of loose curved cells resembling, as WORSDELL points out in the case of *A. Cookii*, the tissue of a stigma. The superficial layer of the integument consists of tangentially elongated cells with dark contents, succeeded by a few layers of long and narrow elements; below these occurs a broader zone of short parenchymatous cells followed by a few layers of narrow and tangentially elongated elements below the limiting layer of cells with dark contents.

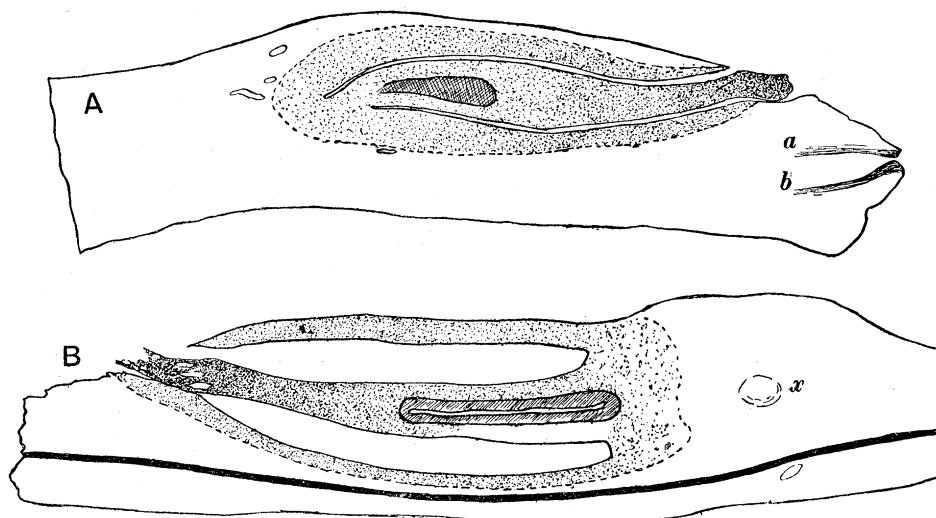


FIG. 26.—A, *Araucaria Rulei*; B, *A. imbricata*.

A mature cone-scale of *Araucaria imbricata*, which reaches a length of 7–8 centims. (fig. 24, K) terminates distally in a narrow upturned lamina; the ligule

extends from the distal end of the seed as a fairly broad band terminating at the edge of the broad portion of the scale in a bluntly-rounded and free apex. In a younger scale the free portion of the ligule is fimbriate as in *A. Rulei*. The integument surrounds the broad micropyle as a lobed margin. On pulling to pieces an old cone of *A. imbricata* we noticed that several seeds had begun to germinate, and a few radicles were found in one case reaching a length of 1 centim. lying between the cone-axis and the bases of the scales.\*

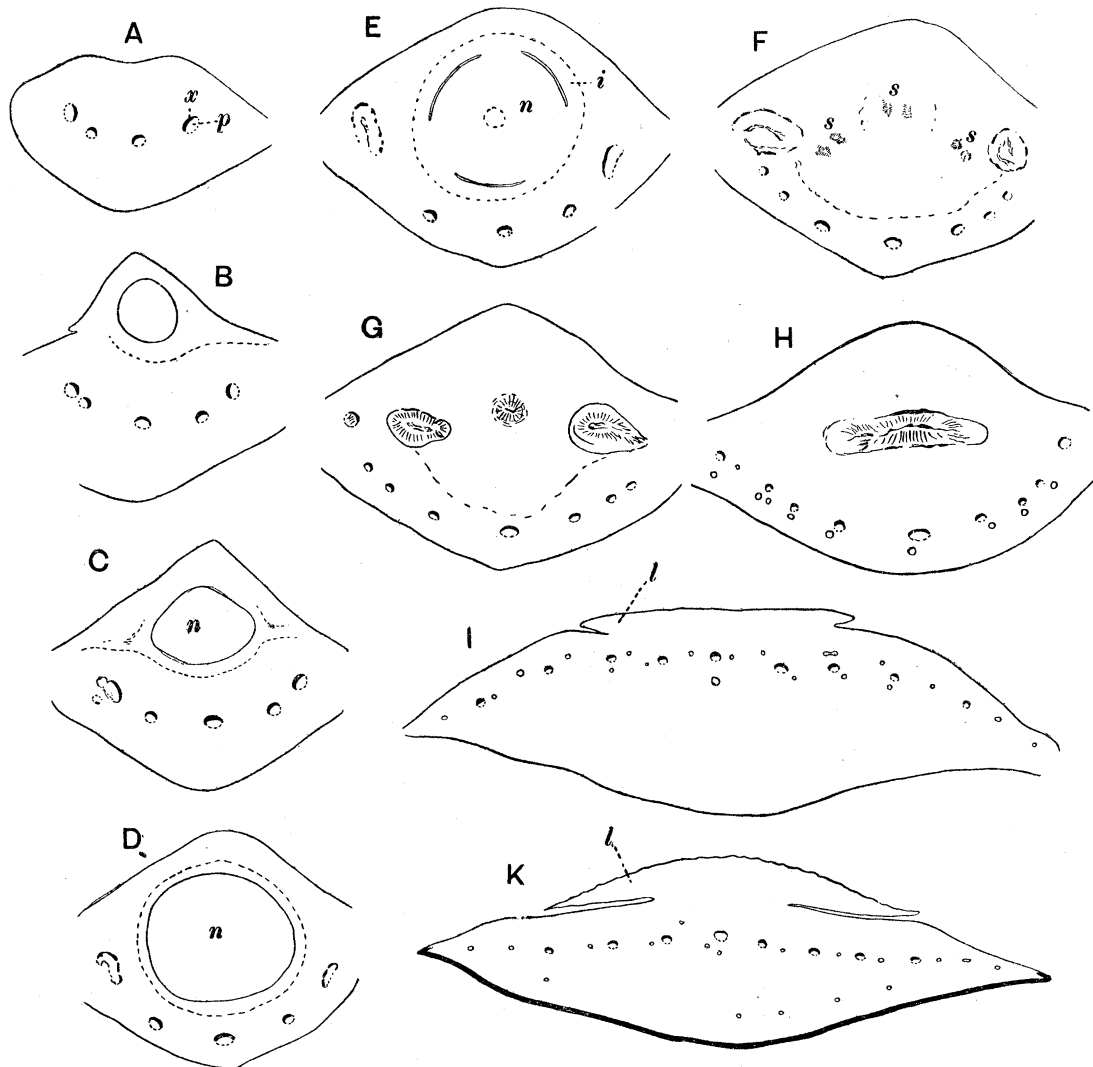


FIG. 27.—A-K, *Araucaria imbricata*.

The vascular bundles in the scales of *A. imbricata* differ in several respects, as regards their course and behaviour, from those in the other species investigated. A single bundle leaves the vascular network (fig. 25, D, 1) of the cone-axis, and in the base of the scale gives off a strand from each side (D, 2 and 3). Later stages

\* Compare germinating spores in the strobilus of *Selaginella rupestris* as figured by LYON (1901), Plate 9, fig. 126.

are represented by figs. 27, A-D. In fig. 27, E, which shows the nucellus, *n*, partially attached to the integument, *i*, the left-hand bundle is seen to be altering its shape, and in succeeding sections it is found to assume an oval form with a central band of crushed protophloem and peripheral groups of xylem tracheids (figs. 27, E, F). The right-hand bundle undergoes a similar change (fig. 27, F). The section shown in fig. 27, F, cut near the base of the nucellus, shows three pairs of strands of long and narrow elements having the appearance of young vascular strands (*s*) pursuing a course oblique to the plane of the section. The next section (fig. 27, G) contains, in addition to the lower series of small collateral bundles, two large concentric strands and a median strand of similar structure, which at the stage represented in G contains no lignified tracheids, but small peripheral groups of xylem elements appear in the succeeding section. The three concentric strands gradually approach one another, and finally coalesce to form the elliptical strand seen in fig. 27, H. The ends of this strand consist of elements for the most part unlignified, lying in an obliquely horizontal plane; at a short distance beyond the section represented in fig. 27, H, this strand dies out. The scale has now assumed a flatter and broader form and the ligule, *l*, is becoming detached at the edges (fig. 27, I). Fig. 27, K, represents a section near the distal end of the scale where the ligule, with the upper edge slightly fimbriate, is almost free. The bundles and canals now appear as in the lamina of a foliage leaf; the lower epidermis contains a few stomata, and there are two or three hypodermal layers of thick-walled fibres; with the exception of the ligular outgrowth the structure of the scale is now practically identical with that of a leaf. The chief difference as regards the bundles of the scale between *Araucaria imbricata* and the other species described consists in the absence of an upper series of collateral strands. The end bundles of the lower series assume a concentric structure, and the resulting strands coalesce to form a central group which soon dies out. The behaviour of the vascular strands in a sterile cone-scale is almost identical with that already described, but we found, as might be expected, that series of sections of different sterile seeds exhibited more or less striking variations. In some cases a few bundles with inverse orientation were met with above the upper series, occupying the position of the upper series which occurs as a normal feature in *A. Cookii* and *A. Rulei*.

Fig. 26, B, represents a cone-scale of *A. imbricata* in median longitudinal section (9 millims. long). A single vascular strand extends the whole length of the portion of scale shown in the drawing; the nucellus, which has shrunk away from the integument, terminates in a dark brown and partially disorganised apex which projects through the micropyle; the small-celled tissue at the base of the nucellus forms a fairly sharp contrast to the ground-tissue of the scale, which contains many large sclerites, and at *x* shows a patch of vascular tissue consisting of a central group of crushed phloem surrounded by xylem tracheids running approximately in the



plane of the section. The vascular tissue below the base of the nucellus bears a fairly close resemblance to the same tissue as seen in a transverse section of the scale; it occurs in the form of more or less oval patches which exhibit a concentric arrangement of the xylem and phloem.

*A. Cookii*.—A cone-scale of this species (fig. 24, g), like others of the *Eutacta* section, is characterised by a broad membranous wing consisting in a mature scale of crushed air-containing tissue with scattered sclerites. The ligule is a conspicuous feature, and in a median longitudinal section of a young scale it is seen to have the form of a narrow outgrowth separated for the greater part of its length from the cone-scale. The micropyle is a long and narrow opening as in the other species described, and the nucellus possesses the characteristic long and narrow beak. The behaviour of the vascular strands in the scale has been fully described by WORSDELL,\* and we can confirm his results.

*A. Bidwillii*.—The cone-scales of this species are distinguished by great breadth and by the thickness of the prominent ligule (fig. 24, l). The two scales represented in fig. 24, L and M, show the broad and massive seed-scale with the acuminate distal end and the broad and stout ligule (*l*) resting on the surface of the scale. WORSDELL† lays stress on the fact that in this species the bundles of the “bract and seminiferous scale arise quite independently from the central cylinder of the cone-axis, and at a wide vertical distance apart.” The course of the two sets of bundles in the cone-scale is similar to that in *A. Cookii*, but there is a marked tendency towards a concentric disposition of the xylem and phloem. WORSDELL notes that two strands of phloem-like tissues were seen penetrating the chalazal part of the ovule; a statement agreeing with our observations in *A. imbricata*. We venture to dissent from this author's conclusion that the separate origin of the bundles which enter the cone-scale from the stele of the cone-axis “assuredly would not be likely to happen if the appendicular organs which they supply represented a single scale.”‡ So far as we are aware, the separate origin of the bundles is peculiar to this species, but in view of the stoutness of the scale we see no fatal objection to the suggestion that, in the course of evolution, bundles which were formerly united at their point of exit from the axis afterwards pursued a separate course to the vascular tissue of the central cylinder. We do not regard the occurrence of concentric vascular strands in *A. imbricata* and *A. Bidwillii* as evidence of an approach to the Cycads. The concentric structure is too frequently met with in cases where the normal structure of the majority of bundles is collateral to be considered as a feature of phylogenetic significance. At the base of an ovule with radial symmetry, as in *A. imbricata* and *A. Bidwillii*, it may be an advantage for the vascular tissue to assume a concentric arrangement; to attach so great an importance to the occurrence of concentric

\* WORSDELL (1899).

† WORSDELL (1899), p. 532.

‡ WORSDELL (1899), p. 535.

strands in a region where the bundles pursue a tortuous course in order to mass the vascular elements near the ovule base, seems to us a strained conclusion. The cone-scales of *A. brasiliensis* (fig. 24, N, o), and the course of the bundles have been described by VAN TIEGHEM, and STRASBURGER has pointed out that in this species the sterile scales possess only one series of vascular strands. STRASBURGER also describes *A. Cunninghamii* and *A. excelsa*, which agree in essentials with *A. Cookii*, as described by WORSDELL and by ourselves. A constant feature in all species examined is the occurrence of two series of bundles, at least in the fertile seeds, and in some cases both series are represented in the seedless scales. We do not regard the upper inverted bundles as evidence favouring the axillary-bud theory of CELAKOVSKY and other authors, but we follow EICHLER in regarding the inverted orientation of the bundles as a normal feature of vascular strands supplying an appendage of a leaf, and we see no adequate grounds for designating the cone-scale of the Araucariæ as other than a leaf.

#### *The Structure of the Ovule and Embryo.*

Our knowledge of the female gametophyte and of the embryogeny of the Araucariæ is far from complete, and through lack of material we are at present unable to add very much to facts already known. Since the publication of STRASBURGER's great work\* on the Coniferæ and Gnetaceæ little has been done towards a complete investigation of the megaspore of the Araucariæ. The chief facts recorded are—(i) the extension of the nucellus as a stigma-like beak into the micropyle,† (ii) the sunken position of the archegonia at the base of funnel-shaped depressions in the prothallus, and (iii) the occurrence of a fan-shaped group of covering cells at the apex of the proembryo. The more recent investigations of GOROSCHANKIN‡ and ARNOLDI§ have supplied further information as to the archegonia and prothallus of *Agathis* and *Araucaria*. Our own material of *Araucaria imbricata* was the most complete, and the following description is based on that species:—

The longitudinal section of the cone-scale, represented diagrammatically in fig. 26, B, illustrates the long and narrow form of the shrunken prothallus and megaspore in a young ovule; at a later stage the megaspore occupies a large proportion of the nucellus, and the latter persists as a partially disorganised apical covering in which remains of pollen-sacs are occasionally seen. The prothallus reaches a length of 1 cm.; it is broad and bluntly rounded at the apex and becomes gradually narrower towards the chalazal end of the ovule; the superficial layer consists of slightly columnar cells. The archegonia are characterised by their deep-seated position and lack of regular arrangement; they occasionally occur in a more or less superficial

\* STRASBURGER (1872).

† WORSDELL (1899); STRASBURGER (1872, 1879).

‡ GOROSCHANKIN (1880).

§ ARNOLDI (1900).

position, but more usually the neck is separated by several layers of cells from the surface of the prothallus; they appear to be confined to the upper region of the megaspore. The archegonia of *Araucaria imbricata* frequently occur in the prothallus without any funnel-shaped depression affording a direct communication with the surface. In this respect they agree with the archegonia of *Sequoia* as described by SHAW,\* COKER,† ARNOLDI,‡ and LAWSON.§ The former author regards the arrangement and large number of the archegonia in *Sequoia* as a primitive character, and we are disposed to apply the same conclusion to *Araucaria* and *Agathis*. LAWSON states that cells near the central axis of the megaspore of *Sequoia* may form initial cells of archegonia, and JÄGER|| notes that in *Taxus baccata* the archegonia become deeply sunk in the prothallus and very rarely occur in the middle of the megaspore. In *Araucaria imbricata* the numerous archegonia appear to be confined to the upper region of the megaspore, but in *Agathis australis* they are said to be spirally disposed through the whole of the endosperm,¶ and may reach a total of sixty.

Another feature characteristic of *Agathis australis* and *Araucaria imbricata* is the large number of neck-cells in the archegonia (fig. 28, c). STRASBURGER\*\* speaks of only 4 cells in the neck of *A. brasiliensis*, but we find two tiers of cells and as many as 12 cells in a single tier of the neck of *A. imbricata* and in *Agathis australis*. GOROSCHANKIN's figures†† show as many as 13 cells in a transverse section of the neck.

Fig. 28, B, shows the upper portion of the megaspore of *A. imbricata* enclosed by the crushed and partially disorganised nucellus; two archegonia are exposed, one of which is cut through in an approximately median plane. A single archegonium is shown in fig. 28, A, about .5 millim. in length, with two neck-cells, seen at *n*; the large egg-cell is surrounded by a layer of jacket-cells, characterised by dark contents and large nuclei. The slightly contracted cytoplasm terminates in a blunt papilla which contain a somewhat ill-defined darker substance, which is in all probability the nucleus of a ventral canal-cell separated by a fairly well-marked division, *a*, in the cytoplasm from the egg-cell.‡‡ The membrane of the large egg-nucleus has shrunk away on one side from the surrounding cytoplasm. The neck in fig. 28, A, appears to be composed of a single tier of cells, but a portion of a tangential wall is seen in the left-hand cell, and in other sections two tiers

\* SHAW (1896).

† COKER (1903).

‡ ARNOLDI (1900), p. 406.

§ LAWSON (1904), Plate 2, fig. 17.

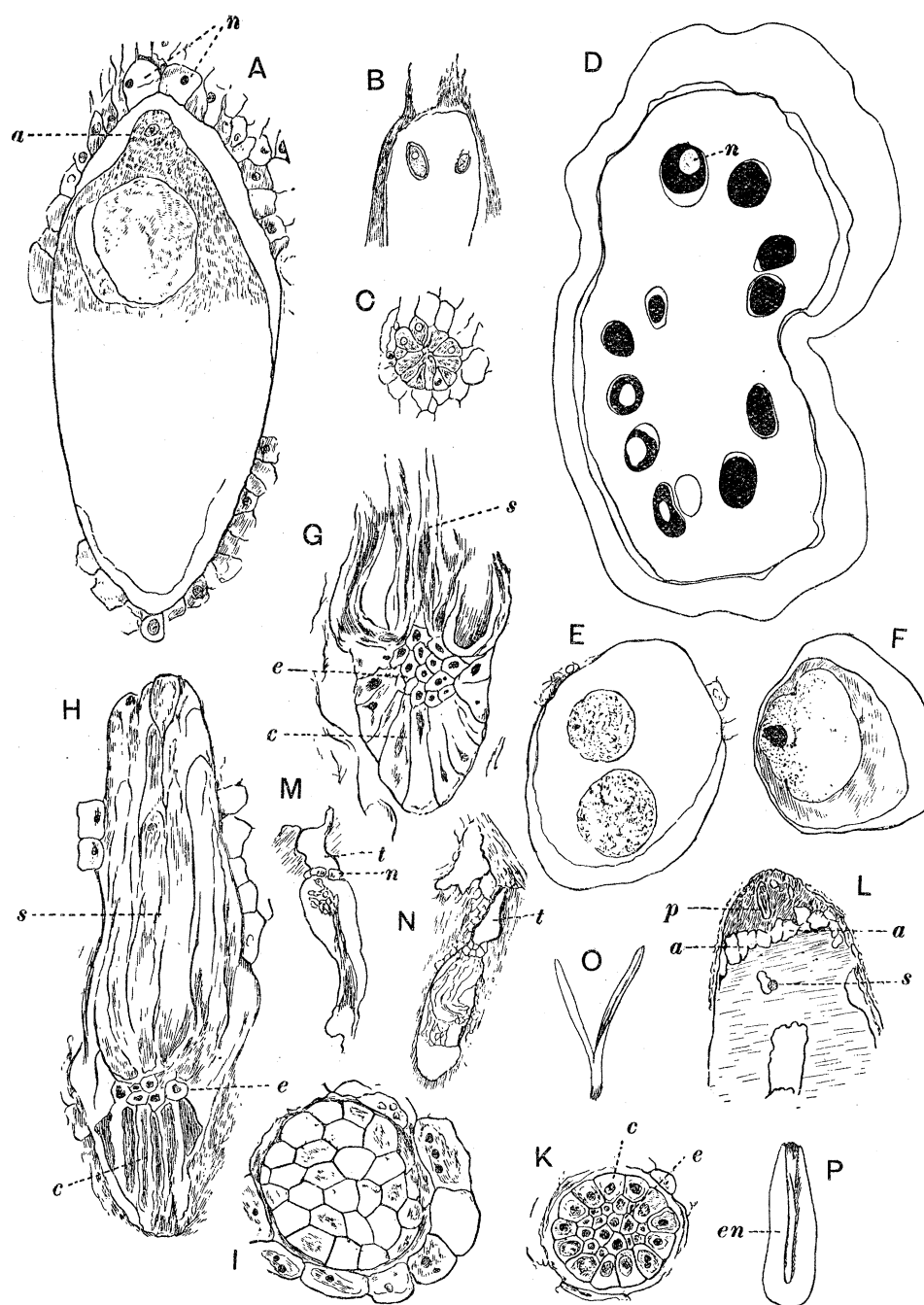
|| JÄGER (1899), Plate 17, fig. 28.

¶ ARNOLDI (1900); GOROSCHANKIN (1880), Plate 6, fig. 44.

\*\* STRASBURGER (1879), p. 150, Plate 20, fig. 63B.

†† GOROSCHANKIN (1880), Plate 6, fig. 46.

‡‡ Cf. GOROSCHANKIN's figure of *Abies sibirica* (1880), Plate 8, fig. 57.

FIG. 28.—*Araucaria imbricata*.

of cells are clearly shown. The number of cells in a tier is considerable; the section represented in fig. 28, c, which may be regarded as approximately transverse to the long axis of the archegonium, shows 12 neck-cells.\* The transverse section (fig. 28, d) illustrates the position occupied by the numerous archegonia, in some of which the large nucleus, *n*, is seen. In a recently-published paper, Mr. R. B. THOMSON has

\* Cf. GOROSCHANKIN (1880), Plate 6, fig. 46 (*Agathis*).

described in detail the megaspore-membrane and tapetum of several species of Cycads and Conifers. In view of his work we have not paid special attention to these structures, nor was our material suitable for such minute anatomical investigations as these alone could throw further light on the subject. THOMSON describes the megaspore-coat of *Agathis australis* as "poorly differentiated structurally at all stages." In *Araucaria imbricata* and *A. brasiliensis* the coat, though much less developed than in *Agathis*, possesses a similar character. He points out that in both genera the tapetum and megaspore-membrane are peculiar, and in this respect, as in many others, the Araucarieæ are clearly marked off from the rest of the Coniferales.\* In one transverse section of a megaspore we noticed two large nuclei of approximately equal size in the cytoplasm of a single egg-cell (fig. 28, E); we think it probable that these may be the male and female nuclei; the nucleus shown in fig. 28, F, presents an appearance suggestive of a male partially absorbed by a female nucleus. The slight difference in size between the two partially-fused nuclei may be considered an argument against their description as male and female.† It is true that the difference in size is usually more marked, but in *Taxodium*, COKER‡ points out that the male nucleus increases in size on its course to the female nucleus, and after contact the former is half as large as the latter. In *Cephalotaxus*§ the difference in size is not much more than that shown in fig. 28, F. In *Sequoia sempervirens*|| the male and female nuclei appear to be approximately equal in size, a fact in favour of our interpretation of the constricted nucleus in *Araucaria imbricata*, shown in the figure.

Some of the ovules examined were found to contain several embryos in different stages of growth; the median portion of the prothallus is often partially destroyed and the cells in this region are distinguished by their slightly darker contents and by a tendency to arrange themselves with their long axes parallel to the long axis of the megaspore. The pro-embryo consists at the distal end of a somewhat fan-shaped group of cells (fig. 28, G, c), with distinct nuclei arranged above and around a group of small cells, e, which represent the embryo proper. Behind the embryo occurs a bundle of long suspensor cells, s, which terminate in a group of rather shorter elements lying in the cavity formerly occupied by the egg-cell.

The group of cells at the tip of the pro-embryo of *Araucaria* (fig. 28, G and H), which are described by STRASBURGER as being thrown off during development of the embryo, are regarded by him as forming a protective cap. A similar covering is formed also in *Cephalotaxus*,¶ and more recently ARNOLDI\*\* has noticed similar

\* THOMSON (1905), p. 26.

† Cf. BLACKMAN (1898) (*Pinus silvestris*), fig. 39, A; LAND (1902) (*Thuja*), Plate 7, fig. 16; LAWSON (1904), (*Cryptomeria*), Plate 30, fig. 44; ROBERTSON (1904), (*Torreya*), Plate 8.

‡ COKER (1903), Plate 8, fig. 102.

§ ARNOLDI (1900), Plate 2, fig. 24.

|| LAWSON (1904), Plate 3, fig. 30.

¶ STRASBURGER (1879), Plate 19.

\*\* ARNOLDI (1900), pp. 467, 468.

cells in *Sciadopitys*; this author suggests a comparison between the apical cap and the protocorm of *Lycopodium cernuum* described by TREUB.\* The comparison instituted by ARNOLDI with the protocorm of *Lycopodium*—"a neutral body" from which the embryo becomes differentiated—does not appear to us convincing. The transverse sections—fig. 28, I, K—represent two neighbouring pro-embryos; in fig. 28, I, the suspensor tubes have been cut through, while in fig. 28, K, there is a central group of embryo-cells, *e*, surrounded by the lateral cap-cells, *c* (*cf.* fig. 28, G and H). The endosperm cells in the neighbourhood of the pro-embryo frequently contain more than one nucleus (fig. 28, I), in some cases as many as four were seen in one cell.

The general tendency is for the pro-embryos to grow through the endosperm along its median axis, and we noticed in one case two pro-embryos lying side by side in the disorganised central region. Fig. 28, L, *p*, represents a pro-embryo which has penetrated into the nucellus, and in a neighbouring section the pro-embryo was seen with one end in the endosperm and the apex boring its way towards the surface of the nucellus. The suspensor of another pro-embryo is seen at *s*, lying to one side of the space formerly occupied by the egg-cell. The nucellus is separated from the endosperm by a space, *a*, bridged across by crushed cell-walls, which may be compared with a similar space described by OLIVER† in certain fossil Gymnospermous seeds as the supra-archegonial gap. Figs. 28, M and N, show portions of two embryos with two neck-cells at *n*; the spaces *t* and *t*, bounded by a fairly thick wall, probably represents the remains of pollen-tubes. A much later stage in the development of the embryo is represented in fig. 28, O and P; these embryos were dissected out of a mass of endosperm obtained from seeds 7·5 centims. long still attached to a cone. In the case of one of these the radicle had begun to push its way through the micropyle. The embryo, which occupies nearly the whole length of the endosperm, has two cotyledons, one of which—especially in the embryo that is shown in fig. 28, O—is slightly shorter than the other.

#### X. FOSSIL ARAUCARIEÆ.

The Coniferales are among the most difficult plants to deal with from the standpoint of the palæobotanist. In the Araucarieæ we have a section of Gymnosperms which by virtue of the possession of well-marked distinguishing features is more easily recognised than other members of the Coniferales. It is true that the records afforded by Permo-Carboniferous and Triassic rocks are by no means convincing as evidence of the existence of the Araucarieæ during the Palæozoic era, although several authors believe that certain Palæozoic genera may be legitimately included in the Araucarieæ. On the other hand, the rocks of the Mesozoic era have afforded ample testimony to the wide distribution and abundance of Araucarian plants.

\* TREUB (1884<sup>2</sup>) (1890).

† OLIVER (1904), Plate 42, fig. 13.

The statement made by Professor JEFFREY\* that "the Abietineæ must be regarded on comparative and morphological grounds as a very ancient order of the Coniferales, and may even be the oldest living representatives of this group," is one to which we cannot subscribe. In determining a question of relative antiquity we must pronounce an opinion on such data as are available, and the consideration entitled to most weight is that based on the records of the rocks, records which we believe point to a conclusion at variance with that which we have quoted. Other considerations, *e.g.*, the relative proportion of primitive characters met with in the recent species of *Agathis* and *Araucaria* are dealt with in the concluding section of this paper.

The available material from which to compile a history of the Araucarieæ consists of (i) petrified wood; (ii) vegetative twigs or leaves preserved as casts or incrustations; (iii) pith-casts or casts exhibiting the external surface of leafless branches; (iv) cones and isolated cone-scales and seeds.

(i) *Petrified Wood*.—The wood of recent species of *Agathis* and *Araucaria* is fortunately characterised by such features as serve as trustworthy tests by which it can be distinguished from that of other Conifers.

There is no doubt that GOTHAN† is amply justified in drawing attention to the worthlessness of many of the determinations of fossil wood as Araucarioid; while admitting the justice of his timely criticism of the neglect of essential characters by authors, we believe that true Araucarian wood is sufficiently abundant to justify our contentions that the Araucariales played a dominant rôle in the Mesozoic vegetation.

On the other hand, the wood of the Palæozoic genus *Cordaite*s is practically identical with that of the recent Araucarieæ; the greater number of pits on the radial walls of the tracheids of this extinct type—a feature dealt with at length by PENHALLOW‡ and GOTHAN§—cannot be utilised as a safe means of identification.

It has been generally recognised that much of the Palæozoic wood described under KRAUS' generic name *Araucarioxylon* must be ascribed to *Cordaite*s; but it by no means follows that all Palæozoic wood of the Araucarian type can be safely referred to *Cordaite*s. It has been suggested by FELIX and others that the term *Araucarioxylon* may be conveniently restricted to wood from Mesozoic and Tertiary strata, geological periods which have afforded no certain evidence of the existence of *Cordaite*s, the genus *Dadoxylon* being retained for examples of the same type of wood from Palæozoic rocks which cannot be confidently assigned to *Cordaite*s. The question of nomenclature in regard to fossil wood possessing Araucarian characters has been fully discussed in a recently published paper by GOTHAN; this author prefers to class all Araucarioid fossil wood under the generic designation *Dadoxylon*.||

\* JEFFREY (1905), p. 33.

† GOTHAN (1905), p. 38.

‡ PENHALLOW (1904), p. 255; (1900).

§ GOTHAN (1905), p. 19.

|| GOTHAN (1905), p. 29.

So far, then, as regards Palæozoic records, wood possessing Araucarian characters does not in itself afford evidence of the existence of the Araucariæ. SCOTT has expressed the view that the secondary wood alone is of little value as a guide to affinity; this statement would seem to imply that secondary wood of the Araucarian type from Mesozoic rocks is evidence of minor importance in connection with the past history of the Araucariæ. While admitting the truth of this statement so far as it concerns Palæozoic specimens, we are disposed to accept Mesozoic examples as indications of the existence of plants nearly related to *Araucaria* and *Agathis*. We are, however, not restricted to this kind of testimony; our conclusions as to the age of the Araucariæ are based on evidence afforded by different classes of facts.

(ii) *Vegetative Twigs*.—The botanical value of vegetative twigs is frequently misleading, and there is no doubt that many of the identifications of fossil Conifers founded on imperfectly preserved branches are valueless. Among recent Conifers which exhibit a fairly close resemblance to Araucarian shoots of the Eutacta section we may cite *Cryptomeria japonica* and certain species of *Dacrydium*. Among the numerous Coniferous branches of Mesozoic age simulating *Araucaria* we have species of *Brachyphyllum*,\* *Cheirolepis*, *Sphenolepidium*, and other artificial genera.

(iii) *Stem-casts, etc.*—Fossil casts are occasionally found which bear so close a resemblance in their surface markings to stems of recent genera that one is tempted to hazard a guess as to their affinity. If we do not allow our opinion the weight of a committal generic designation no harm is done. As an instance of this class of evidence we may quote the Mesozoic stems to which the generic name *Benstedtia*† has been applied, with the suggestion that they may be Cycadean; in one instance a French author has assigned to this class of stem the generic name *Coniferocaulon*,‡ expressing his opinion that the surface characters point to a comparison with Araucarian stems. The stem-casts described by FLICHE as *Coniferocaulon colymbæforme* do not afford evidence of value as to the existence of Araucariæ and at best—assuming that FLICHE's interpretation is correct—fossils of this kind could be used only as collateral evidence of no intrinsic value unless supported by more satisfactory data.

(iv) *Cones, etc.*—The cone-scales of recent Araucariæ are clearly distinguished from those of other members of the Coniferales, and may therefore be accepted as trustworthy tests.

As a matter of convenience, we have considered the palæobotanical data having reference to the geological history of *Agathis* in a special section at the end of our survey of the evidence bearing on the existence in former epochs of plants more or less closely allied to the genus *Araucaria*.

\* See footnote §, p. 382.

† SEWARD (1895), Plate 12; (1896) Plate 14; (1903<sup>2</sup>), p. 34.

‡ FLICHE (1900<sup>2</sup>), figs. 1–3.



## a. ARAUCARIA.

*Palæozoic Records.*—The most convenient method of summarising the facts gleaned from a study of Palæozoic plants which have a bearing on the question at issue is to consider briefly such genera as have been either definitely referred to the Araucarieæ, or regarded as probably referable to that division of the Coniferales.

*Walchia.*—The generic name *Walchia*, instituted by STERNBERG, is applied to branches met with in the upper members of the Carboniferous system and in strata of Permian age. The sterile shoots are usually in habit and in foliar characters practically identical with those of recent species of the Eutacta section of *Araucaria*. The close resemblance between *Walchia piniformis* and *Araucaria excelsa* was recognised by BRONGNIART in 1849.\* Pith-casts of *Walchia* also resemble those of recent Araucarian branches. The evidence afforded by the reproductive shoots is unfortunately indecisive and somewhat conflicting; some examples have been described as bearing cones consisting of single-seeded scales; others, again, appear to have borne seeds between the foliage leaves without well defined scales. As RENAULT† has suggested, it is not improbable that under STERNBERG's genus more than one generic type has been included.

Many of the published figures of reproductive shoots of *Walchia* convey no satisfactory impression of the morphology of the strobilus, but reference may be made to the drawings of *W. filiciformis*‡ published by ZEILLER in his monograph of the Brive flora, in which the scales are shown to bear single seeds. FLICHE§ has described a fossil wood from Permian strata of the Vosges (*Araucarites Valdaïolense* Moug.) which he regards as Araucarian and as probably the wood of *Walchia*: the bark bears spirally disposed leaf-cushions. In his description of the petrified Permian forest in the neighbourhood of Chemnitz, STERZEL|| mentions the occurrence of *Walchia* twigs in association with wood of the Araucarian type. GOTHAN¶ incidentally speaks of *Walchia* as a genus which has been wrongly referred to the Araucarieæ. We agree with ZEILLER as to the probability of a real affinity between *Walchia* and the genus *Araucaria*.

*Schizodendron (Tylodendron).* The generic name *Tylodendron* was originally applied by WEISS to specimens from the Upper Carboniferous rocks of Germany and

\* BRONGNIART (1849), p. 70.

† ZEILLER (1892), p. 99. Plate 15, fig. 3. BERGERON (1884) has figured good examples of *Walchia* strobili, showing the external features. See also GOEPPERT (1864), Plates 48–52; GEINITZ (1861), Plate 31; SAPORTA (1884), p. 392.

‡ RENAULT (1896), p. 353.

§ FLICHE (1903), p. 14, fig. 2.

|| STERZEL (1896).

¶ GOTHAN (1905), p. 13.

POTONIÉ\* afterwards demonstrated that the surface-features which WEISS described as leaf-bases were those of a medullary cast. ZEILLER† subsequently revived EICHWALD's generic name *Schizodendron* which was applied to casts, generically identical with those described by WEISS, as having priority over *Tylodendron*. The close resemblance between *Tylodendron* and the casts of the pith of *Araucaria* and *Agathis*, both as regards the casts of the medullary rays and leaf-traces, and in the peculiar increase in diameter which in the recent stems characterises the pith in the region of the branch "whorls," is clearly shown in POTONIÉ's figures. Petrified wood found in connection with *Tylodendron* is of the Araucarian type. In all probability, therefore, *Schizodendron* represents the pith-cast of a Palæozoic plant—possibly *Walchia*, a genus which would seem to include species bearing a greater similarity to *Araucaria* than to any other existing genus. ZEILLER‡, who holds the view that *Schizodendron* stands for pith-casts of *Walchia*, mentions the fact that in many places *Walchia* is the only Gymnosperm found in association with the pith-casts.

*Gomphostrobus*.—This genus was instituted by MARION§ for certain fossils from the Permian of Lodève, possessing vegetative characters bearing a resemblance to those of *Walchia* and distinguished by monospermic deciduous cone-scales with a bifurcated lamina. STERZEL|| states that he has found *Gomphostrobus* at Chemnitz in association with *Araucarioxylon* wood. Figures of this plant of somewhat doubtful affinity may be found in the works of POTONIÉ,¶ ZEILLER, and others.

A portion of a vegetative branch bearing leaves like those of *Araucaria imbricata* has been recently described by ZEILLER from the Lower Gondwana rocks (Permian-Carboniferous) of India as *Araucarites Oldhami*. We have more satisfactory evidence of the existence of Araucarian plants in India in the Jurassic period: ZEILLER's Palæozoic species belongs to the class of fossils which cannot be identified with certainty.

*Trias*.—The genus *Albertia*,\*\* established by SCHIMPER and MOUGEOT for vegetative branches from Triassic rocks of the Vosges, is characterised by oval leaves decurrent at the base and traversed by numerous veins, externally similar to the leaves of *Agathis* and certain species of *Araucaria*. Seeing that the reproductive organs are very imperfectly known, we cannot quote this genus as contributing to our knowledge of the Araucariæ.

*Voltzia*.—This genus, established by BRONGNIART in 1828,†† has been recorded from Permian rocks, but it is more particularly characteristic of the Triassic

\* POTONIÉ (1888): (1893).

† ZEILLER (1892), p. 102; (1900), p. 262.

‡ ZEILLER (1892), p. 103.

§ MARION (1890), p. 892.

|| STERZEL (1896), p. 892.

¶ POTONIÉ (1893).

\*\* SCHIMPER and MOUGEOT (1844), p. 14, Plates 2-5; SCHIMPER (1874), Atlas, Plate 74.

†† BRONGNIART (1828).

formation. The vegetative shoots agree closely in habit with those of the Norfolk Island Pine; the cones, while resembling externally those of certain Abietineæ, do not exhibit any structural feature which justifies a recognition of the genus as a member of that section of the Coniferales. As SOLMS-LAUBACH says,\* "the flat-scales seem to point to affinity with the typical *Araucaria*, the structure of the seeds with *Sequoia*." The essential features are, however, too little known to admit of the inclusion of *Voltzia* among the fossil representatives of the Araucarieæ. It is of interest to note that specimens of *Voltzia heterophylla* in the Strassburg Museum† exhibit pith-casts of a type apparently identical with *Tylodendron* (*Schizodendron*).

In addition to such genera as *Albertia* and *Voltzia*, Triassic rocks have afforded somewhat similar types of vegetative twigs described under *Palissya*, *Brachyphyllum*, and other provisional designations, which exhibit a superficial resemblance to Araucarian shoots. The term *Araucarites* as used by several authors is often misleading; among Triassic fossils to which this name has been applied without adequate reason we may mention *Araucarites? pennsylvanicus*, FONT., and *A. Yorkensis*, FONT., fragmentary fossils from the Triassic rocks of Pennsylvania.‡ Specimens of petrified wood described by KNOWLTON, from North Carolina as *Araucarioxylon virginianum* present distinct Araucarian characters,§ but *A. arizonicum*,|| described by the same authors from the Trias of New Mexico is less satisfactory.

*Ullmannia*.—The Permian fossils included under this designation are usually met with in the form of vegetative shoots bearing thick spirally disposed leaves suggesting a comparison with the Eutacta species of *Araucaria*. The cones are represented only by imperfect specimens which do not throw any clear light on the position of the genus.¶ A specimen of petrified wood of *Ullmannia* from Ilmenau figured by SCHENK exhibits a point of agreement with the Araucarieæ in having contiguous multiseriate pits on the radial walls of the tracheids. In his account of the leaf-structure of this genus, SOLMS-LAUBACH notes that the transfusion-tracheids in the leaves are characterised by reticulate thickening bands, and do not agree, therefore, with those in Araucarieæ; it has, however, been shown that this character is not inconsistent with an Araucarian affinity. We must leave *Ullmannia* as a Palæozoic Gymnosperm which possesses Araucarian characters, but cannot without further evidence be assigned with certainty to a definite position.

\* SOLMS-LAUBACH (1891), p. 68.

† SEWARD (1890), p. 219; BLANCKENHORN (1886), Plate 32. For references to literature relating to *Voltzia*, see SCHÜTZE (1901).

‡ WARD (1900), p. 253.

§ *Ibid.*, Plate 37, p. 274.

|| FONTAINE and KNOWLTON (1890), p. 285.

¶ SAPORTA (1884), p. 235.

Among other descriptions of possible Triassic representatives of the Araucariæ, reference may be made to SCHENK's designation of specimens from the Muschelkalk of RECOARO,\* some of which have the form of pith-casts like those of *Schizodendron*, while others, both vegetative twigs and cones, are compared with recent species of *Araucaria*. Although we have no absolute proof of the correctness of SCHENK's view, we believe that in this as in other cases the evidence, so far as it goes, points to the probable existence of Araucarian plants in the Triassic vegetation.

### *Rhætic and Jurassic.*

*Rhætic.*—The Rhætic floras of Scania, Franconia, North America, Tonkin, and other regions, supply little information of any real value as to the presence of Araucarian species. It is by no means unlikely that the close resemblance in habit between the vegetative twigs described by SCHENK,† NATHORST,‡ and others as species of *Brachyphyllum*, *Palissya*, etc., and branches of recent species of *Araucaria* may be more than a mere superficial agreement, but in the absence of trustworthy criteria we cannot quote these examples as contributions to our knowledge of the past history of the Araucariæ. It is possible, as ZEILLER§ suggests, that some of the imperfect cones which he records from Tonkin may be allied to the recent *Araucaria*, but more than this cannot be said. The specimen represented by a crude drawing in FONTAINE's monograph on the older Mesozoic vegetation of Virginia|| as *Araucarites carolinensis* is much too fragmentary to have any claim to the generic designation employed. The petrified wood from Tonkin named by CRIÉ *Araucarioxylon Zeilleri* and referred to by ZEILLER,¶ although probably Araucarian, cannot be quoted with confidence on the evidence so far adduced. From the Burrum Formation ("Lower Trias-Jura"), Queensland, SHIRLEY\*\* has described petrified wood under the name *Araucarioxylon Randsi*, which appears to possess Araucarian characters.

From Jurassic rocks several examples of vegetative shoots and cones have been described which there is every reason to assign to that section of the Gymnosperms. We have no good reason for assuming that the genus *Cordaites* persisted into the Jurassic era, and in view of the collateral evidence of cones and branches, we may safely assign wood of the Araucarian type from Liassic and overlying strata to the Araucariæ.

*British Liassic Araucariæ.*—The generic name *Pagiophyllum* is frequently

\* SCHENK (1868).

† SCHENK (1867), Plate 43.

‡ NATHORST (1878), Plates 23, 24.

§ ZEILLER (1903), pp. 212 *et seq.*, Plate 1.

|| FONTAINE (1883), Plate 52, fig. 4.

¶ ZEILLER (1903), p. 221.

\*\* SHIRLEY (1898), p. 14.

applied to vegetative shoots from Mesozoic rocks exhibiting the habit and leaf-characters of *Araucaria excelsa* and allied species. Some authors use the term *Araucarites* in preference to the form-genus *Pagiophyllum* as denoting an affinity which they believe to be well established. The genus *Pagiophyllum* illustrates the wide distribution of a Jurassic type, which though not proved to be Araucarian is, in all probability, correctly referred to that division of the Gymnosperms; it is recorded from Britain, France, Germany, Portugal, Bornholm, North America, Spitzbergen, and elsewhere.\* *Pagiophyllum peregrinum*, originally described by LINDLEY and HUTTON as *Araucarites peregrinus*,† represents a common species of Liassic Conifers. A comparison of this type with branches of *Araucaria excelsa*, *A. Rulei*, and other species demonstrates a practical identity between the recent and extinct forms; the stout falcate leaves of the fossil specimens, with rows of stomata often recognisable on the carbonised lamina, are precisely the same as those of existing Araucarias. It is unfortunate that no thoroughly satisfactory flowers have so far been found in connection with *Pagiophyllum* twigs, but such evidence as we have is not opposed to an Araucarian affinity.‡ From the Yorkshire Lias, near Whitby, petrified wood, having undoubted Araucarian characteristics, has been described by WITHAM and more recent writers.

*Araucarioxylon Lindleyi*, which has recently been redescribed, affords a good example of Liassic Araucarian wood.§ It is, moreover, very probable that the Whitby jet has in large measure been formed from the wood of Araucarian trees.|| A new genus *Araucariopsis* was instituted by CASPARY¶ for fossil wood found near Königsberg with Jurassic boulders, and characterised by the presence of resin-parenchyma, in addition to the Araucarian type of tracheids. As GOTHAN\*\* points out, this peculiarity is hardly sufficient reason for the introduction of a new generic name. We have no hesitation in stating that Araucarian plants were well represented in the European Liassic vegetation.

*Inferior Oolite Representatives of the Araucarieæ.*—A specimen described by CARRUTHERS†† in 1869 from Inferior Oolite rocks of Yorkshire, as *Araucarites Phillipsi*, affords a striking example of a Jurassic cone of the Araucarian type. The broad monospermic seeds of this form, frequently met with in collections of Jurassic plants, are practically indistinguishable from the cone-scales of existing species of the Eutacta section of *Araucaria*. Vegetative shoots are also abundant which may, with a considerable degree of confidence, be referred to the Araucarieæ.

\* See SEWARD (1900), pp. 291, 303, 305; (1904) p. 164.

† LINDLEY and HUTTON (1833), Plate 88. See SEWARD (1904), p. 48.

‡ ZEILLER (1900), p. 264, describes the scales as monospermic.

§ SEWARD (1904), p. 56, Plates 6, 7.

|| *Ibid.*, p. 62.

¶ TRIEBEL and CASPARY (1889), p. 81, Plates 14, 15.

\*\* GOTHAN (1905), p. 37.

†† CARRUTHERS (1869), Plate 2, figs. 7–9.

A species described by BUNBURY\* in 1851 as *Cryptomerites* (?) *divaricatus*, bears a marked similarity to *Araucaria Cunninghamii* and *A. excelsa*, as recognised by BUNBURY and by NATHORST. Another Jurassic form from Yorkshire—*Nageiopsis anglica*†—characterised by two-ranked, broadly linear leaves, agrees closely with *Araucaria Bidwillii*, and with numerous vegetative shoots described by FONTAINE as species of *Nageiopsis* from the Potomac beds of America.‡ Another abundant Jurassic species is one originally named by BRONGNIART *Lycopodites Williamsoni*, and subsequently referred to HEER's genus *Pagiophyllum*§; the shoots of this species are of similar type to those of the somewhat older *P. peregrinum*; both male and female cones occur, but the preservation is not sufficiently good to enable us to give a detailed diagnosis.

The most convincing evidence of the existence of the Araucarieæ in the Inferior Oolite period is afforded by cones from various localities in Yorkshire, Northamptonshire, and elsewhere. This is not the place to discuss specific characters, but the important point is that several fossil cones have been found which are characterised by a stout central axis bearing broad monospermic scales, and corresponding in all respects, so far as we can judge, with those of recent species of *Araucaria*. As examples of well-preserved Jurassic cones we may cite: *Araucarites sphaerocarpus* (CARR.), *A. ooliticus* (CARR.), *A. Brodei* (CARR.)||; these and other examples lead us to assert with confidence that the Jurassic vegetation of the northern hemisphere was rich in Conifers of the Araucarian type. Under the name *Araucarites* sp. specimens of cones have been described from the Wealden strata of Sussex which may safely be regarded as Araucarian fossils, referred by CARRUTHERS to the genus *Kaidocarpus*, and some of those originally described as Cycadean cones¶ afford other instances of the prevalence in the Wealden vegetation, a vegetation in close agreement with that of the Inferior Oolite period, of Araucarian plants.

Among examples of Jurassic Araucarian cones and seeds recorded from extra-British localities the following may be mentioned :—

*Araucarites cutchensis*, FEIST., India\*\* and Madagascar.††

*A. macropterus*, FEIST.,‡‡ Jurassic of India.

*A. moreauna*, SAP.,§§ Corallian of France.

\* BUNBURY (1851). See also SEWARD (1900), p. 287.

† SEWARD (1900), p. 291, Plate 10.

‡ FONTAINE (1889), Plates 77, 86, etc.

§ SEWARD (1900), p. 291, Plate 10.

|| SEWARD (1904), pp. 130 *et seq.*, Plates 12, 13, text-figs. 16–18.

¶ SEWARD (1895, 1896).

\*\* FEISTMANTEL (1876), Plates 7–12: (1877) Plate 14; (1879) Plates 14–16.

†† ZEILLER (1900).

‡‡ FEISTMANTEL (1877), Plate 8; (1879) Plate 16.

§§ SAPORTA (1884), Plates 56, 57.

- Araucarites* sp.,\* Jurassic of Victoria (Australia).  
*A. microphylla*, Sap.,† Kimeridgien of France.  
*A. Falsani*, SAP.  
*A. Rogersi*, SEW.,‡ from Wealden rocks of Cape Colony.

An interesting addition to the Jurassic Floras of the world has been made by the recent Swedish Expedition under NORDENSKJÖLD. ANDERSON discovered several Jurassic species in latitude 63° 15' S. and longitude 57° E. in Louis Phillipe Land; among them were cone-scales referred by NATHORST§ to *Araucarites cutchensis*, an Indian species of Feistmantel.

While we believe that the Araucarieæ were strongly represented in the Jurassic and Wealden floras we cannot agree with the statement by LESTER WARD that "all the fossil wood from the English Wealden localities, including the Purbeck, is of the Araucarian type."|| This author has applied the name *Araucarioxylon antediluvianum*¶ to a fossil stem from the Purbeck beds of Portland, which is a conspicuous object against the side of a house in Portland; but there is no satisfactory evidence to justify the use of this generic title. Similarly, KNOWLTON's species *A. Wallacei* and *A. Webbii*,\*\* from Portland, and from the Wealden of the Isle of Wight respectively, are founded on imperfectly petrified material which does not admit of satisfactory diagnosis.

*Cretaceous.*††—The following have been selected as examples of records of Araucarian plants from Cretaceous rocks which, though by no means constituting a complete list, may serve to illustrate the distribution of the Araucarieæ during the Cretaceous period (see table, p. 380).

The species *Araucarioxylon armeniacum*, founded by GÜRICH‡‡ on material from Cretaceous rocks in the Caucasus, is too doubtful to accept as evidence.

*Tertiary.*—Seeing that the various sections of the Coniferales are known to have existed during the Cretaceous (excluding the Wealden) and Tertiary era it is less important for our present purpose to examine in detail the records obtained from these formations. In the case of Jurassic and Triassic rocks we are more directly concerned with the occurrence of the Araucarieæ in floras in which the Abietineæ are not known to have played a prominent part.

\* SEWARD (1904<sup>2</sup>), p. 181, Plate 19.

† SAPORTA (1884), Plate 58.

‡ SEWARD (1903), p. 37, Plate 6, figs. 4 to 7.

§ NATHORST (1904).

|| WARD (1896), p. 491. For a description of petrified Wealden wood of the *Pinites* type, see SEWARD (1896<sup>2</sup>).

¶ *Ibid.*, p. 490, Plate 102, fig. 1.

\*\* *Ibid.*, pp. 495, 406, Plate 102.

†† See footnote §, p. 382.

‡‡ GÜRICH (1885). See remarks by GOTHAN (1905), p. 37.

Name.	Remarks.	Locality.	Reference.
<i>Araucarioxylon barremianum</i> .	The evidence of Araucarian characters is not quite convincing, but in all probability the generic designation is correct	—	FLICHE (1900)
<i>Araucarioxylon Madagascariense</i>	Ditto ditto	Madagascar.	FLICHE (1900)
<i>Araucarioxylon albianum</i> .	Undoubtedly Araucarian . . . . .	—	FLICHE (1897)
<i>Araucarites patagonica</i> . .	Cone-scale; no figure published . . .	Patagonia .	KURTZ (1899)
<i>Sarcostrobilus Paulini</i> . . .	In all probability an Araucarian cone .	France . .	FLICHE (1900)
<i>Araucarioxylon gardoniense</i> .	Quoted by FLICHE as having been described by CRIÉ from the Cenomanien of Ile D'Aix	France . .	FLICHE (1897)
<i>Araucaria cretacea</i> . . . .	Cone . . . . .	France . .	SCHIMPER (1876) FLICHE (1896)
<i>Araucarites inflatus</i> . . . .	We have not seen the figures, but the characters mentioned in the diagnosis indicate an Araucarian wood	Russia . .	KRENDOWSKY (1881)
<i>Araucarites Wyomingensis</i> .	Cone-scales from the Neocomian of Dakota	Dakota . .	WARD (1899)
<i>Araucaria referta</i> . . . . .	Cones from the Albien of France . .	France . .	FLICHE (1896)
<i>A. Revigniacensis</i> . . . . .			
<i>A. Insulinensis</i> . . . . .			
<i>Araucarites ovatus</i> . . . . .	Cretaceous. Founded on vegetative shoots bearing leaves like those of <i>Araucaria imbricata</i>	New Jersey.	HOLLICK (1897) BERRY* (1903)

Several of the Tertiary fossils referred to *Araucarites* are vegetative twigs which in themselves do not suffice to demonstrate the existence of the Araucarian type. From these we select the following:—

*Araucaria Nathorsti*, DUSÉN,\* possibly Oligocene in age, from Magellan Straits; twigs bearing a close resemblance to *A. imbricata*.

*Araucaria Goepperti*† (STERNB.), from the Eocene of Bournemouth; branches similar to *A. excelsa*.

*Araucaria Haastii*, ETTINGSHAUSEN,‡ from New Zealand, founded on branches similar to *A. imbricata* and *A. Muelleri*. ETTINGSHAUSEN mentions the occurrence of petrified wood of the Araucarian type, but there is no proof that this belongs to the foliage shoots.

Among Tertiary plants found in Seymour Island (latitude 64° 15' S.), by Captain LARSEN, a member of the Swedish Antarctic Expedition, NATHORST§ mentions a leaf very similar to those of *Araucaria brasiliensis*, which may be referable to *Araucarites*.

\* This author considers HOLLICK's species should possibly be referred to *Agathis*.

† DUSÉN (1899), p. 105, Plate 12.

‡ GARDNER (1886), Plates 11, 12.

§ ETTINGSHAUSEN (1887), p. 14, Plates 2 and 6.

|| NATHORST (1904).



Among records of petrified wood of Tertiary age possessing Araucarian features the following may suffice :—

*Araucarioxylon*, sp. KRASSER,\* from Leopoldsberg near Klosternemberg.

*Araucarioxylon Schleinitzii*, GOPPERT,† from Kerguelen Island.

*Araucarioxylon Doeringii*, CONW., wood from Oligocene rocks from Fresno-Memoco (Rio Negro).‡

#### b. AGATHIS.

Various more or less fragmentary fossils have been referred to the genus *Dammara*, or at least compared with the recent species, but neglecting specimens which are too imperfect to be determined with certainty, our knowledge of the geological history of *Agathis* is practically *nil*. Certain globose cone-like fossils from the Cretaceous rocks of Bohemia have been described and figured by CORDA, SCHIMPER, and others, as species of *Dammarites*, but VELENOVSKY,§ after an examination of material in the Prague collections, has expressed the opinion that the “cones” are in reality stems, the apparent cone-scales being the thick basal portions of leaves with a long strap-shaped lamina like that of *Cordaites*. We share with ZEILLER a lack of conviction as to the correctness of VELENOVSKY’S conclusions. It is at least certain that we have no adequate grounds for referring the Bohemian genus *Krannera* to the Araucarieæ. As one of us|| has elsewhere suggested, the leaves of *Krannera mirabilis* are probably identical with *Zamites megaphyllum* from the Stonesfield strata of England; VELENOVSKY¶ has also suggested this comparison. Among fossil leaves described as *Dammarites* or *Dammara* the following may be mentioned as examples of fossils referred on insufficient grounds to the Araucarieæ :—

Specimens of large leaves like those of recent species of *Agathis* described by LESQUEREUX from the Dakota group of North America\*\* as *Dammarites caudatus* and *D. emarginatus*; also *Dammarophyllum striatum* (VEL.), referred to this genus by FRIČ and BAYER in their monograph on Cretaceous plants from Bohemia.††

In addition to leaves, certain scale-like bodies have been referred by some authors to *Dammara* on the strength of a supposed resemblance to the cone-scales of recent species. We fail to recognise any sufficient reason for this comparison. The following are examples of these supposed cone-scales :—

\* KRASSER (1896), p. 423.

† SCHENK in ZITTEL (1890), p. 869, and GOEPPERT (1881), p. 28.

‡ CONWENTZ (1885).

§ VELENOVSKY (1885), Plate 1; FRIČ and BAYER (1901), p. 94, fig. 45.

|| SEWARD (1904), p. 111.

¶ VELENOVSKY (1885), p. 4, footnote.

\*\* LESQUEREUX (1891), p. 32, Plate 1, figs. 9–11.

†† FRIČ and BAYER (1901), p. 96, fig. 48.

*Dammara borealis*,\* HEER, and *D. microlepis*,† HEER, from the Cretaceous (Atane) beds of Greenland; also *D. macrosperma*,‡ HEER, from the Cretaceous (Patoot) beds of Greenland.

HOLLICK§ has described and figured fragmentary fossils from several Cretaceous localities on the East Coast of North America as species of *Dammara*. From Block Island he describes specimens with some hesitation as *Dammara microlepis*, HEER;|| HEER's species *D. borealis* he records from Chappaquidick Island,¶ Long Island, and other localities, and from Cretaceous Clays of New Jersey the same author describes a fragmentary fossil as *Dammara* (?) *Cliffwoodensis*.\*\* This species is recorded also by BERRY†† from Cretaceous rocks in New Jersey; he speaks of it, small kite-like scales or problematical fossils, and quotes NEWBERRY'S well-founded doubts as to their relationship with *Agathis*.

Cretaceous fossils from Bohemia assigned by FRIČ and BAYER‡‡ to *Dammara borealis* belong to the same category of specimens too imperfect to describe by the name of an existing genus. The small scale-like bodies described by HEER, HOLLICK, and others, as *Dammarites*, have been referred also to *Eucalyptus*—e.g., *Eucalyptus Geinitzii*, HEER, figured by KRASSER§§ from the Cretaceous of Moravia.

ETTINGSHAUSEN has named some fragmentary leaves and very imperfect scales from Tertiary rocks of Australia *Dammara intermedia*, and other leaves *D. podozamioides*;||| from Tertiary strata of New Zealand he has described some leaves, and a specimen which may be a cone of the *Agathis* type as *D. Oweni*

\* HEER (1882), p. 54, Plate 37, fig. 5.

† *Ibid.*, p. 55, Plate 40, fig. 5.

‡ HEER (1883), p. 17, Plate 53, fig. 11.

§ Since this was written, a paper has been published by A. HOLLICK and E. C. JEFFREY in the 'American Naturalist' (vol. xl, No. 471, March, 1906), containing a description of specimens of kite-shaped scales, referred to *Dammara microlepis*, HEER (?) from Cretaceous clays of Staten Island, New York, and Block Island. Each scale bore three seeds, and is characterised by an arrangement of vascular bundles showing a close resemblance to that in scales of recent species of *Agathis*. The scales are referred to a new genus, and named *Protodammara speciosa*. The paper contains a résumé of the records of fossils identified as *Agathis* scales. The authors also describe the structure of fragments of *Brachyphyllum* twigs, which they believe to have been the shoots of the tree bearing the *Protodammara* scales: the anatomical characters are undoubtedly Araucarian. Associated fragments of lignite were found to possess the characteristic Araucarian structure; of the two types described, one is regarded as the wood of *Protodammara*, and the other is said to be more nearly allied anatomically to existing species of Araucariæ.

|| HOLLICK (1898), p. 57, Plate 3, fig. 9.

¶ HOLLICK (1902), p. 402, Plate 42, fig. 6.

\*\* HOLLICK (1897), p. 128, Plate 11, figs. 5-8.

†† BERRY (1903), p. 61, Plate 48.

‡‡ FRIČ and BAYER (1901), p. 95, fig. 47.

§§ KRASSER (1896<sup>2</sup>), Plate 16, figs. 3 and 6.

||| ETTINGSHAUSEN (1886), pp. 11, 12, Plate 8.

and *D. uninervis*.\* While recognising that some of these determinations may be correct, we prefer to regard the fossils as too doubtful to refer with certainty to the Araucarieæ. GARDNER† has figured a specimen from the Middle Bagshot beds of Bournemouth as a “leaf suggesting *Agathis*,” but it is too fragmentary for identification.

We have stated that the available data from which to write the past history of distribution of plants identical with, or closely allied to, *Agathis* are very meagre: there is, however, one genus of plants ranging from the Rhætic to the middle of the Cretaceous period which may in part at least represent forms belonging to the Araucarieæ. This is the genus *Podozamites* which was instituted in 1843 by BRAUN‡ for specimens of Rhætic age, which he described as fronds bearing lanceolate or oval-lanceolate leaflets gradually narrowed towards the base and with an obtuse or acuminate apex, the lamina being traversed by several simple and bifurcate veins. It has been customary to regard *Podozamites* as a Cycad which played a prominent part in Rhætic and Jurassic floras in almost all parts of the world. It has, however, been suggested§ that these so-called Cycadean fronds may be vegetative shoots of a Conifer having the habit of recent species of *Agathis*. The segments in the fossil specimens appear to be somewhat less regularly disposed than in modern Cycadean fronds, and agree more nearly with the shoots of *Agathis*. As yet we have no certain information as to the nature of the reproductive organs. In a recent Memoir on Mesozoic Cycadophyta, NATHORST|| has expressed the opinion that some specimens which he originally described and figured in 1886¶ were probably borne by a plant possessing foliage of the *Podozamites* type. This conclusion is founded on the association in Rhætic beds of Scania of *Podozamites* with fertile leaflets (*Cycadocarpidium Erdmanni*) and on the similarity of the laminar portion of the seed-bearing organs with the leaves of *Podozamites*. These organs, as shown in NATHORST's figures, have the form of a lanceolate leaf terminating in a short stalk and bearing what appear to be a winged seed on either side at the base of the lamina.

In the absence of specimens attached to an undoubted *Podozamites* axis, we cannot speak with certainty of the correctness of this interpretation; but if NATHORST is proved to be right the *Podozamites* in question can hardly be referred to the Coniferales. Examples of the genus have been figured by SCHENK\*\* and SAPORTA†† on which small scales occur at the proximal end of a *Podozamites* axis.

\* ETTINGSHAUSEN (1887), pp. 15, 16, Plates 1, 2.

† GARDNER (1886), Plate 2, fig. 16.

‡ BRAUN (1843), p. 36.

§ SEWARD (1900), p. 241.

|| NATHORST (1902), p. 8, Plate 1, figs. 5, 6.

¶ NATHORST (1886), p. 91, Plate 26, figs. 15–20.

\*\* SCHENK (1867), Plate 36, fig. 3.

†† SAPORTA (1875), Plate 6, fig. 2.

It has been suggested that the scales may belong to a lateral branch similar to those occasionally produced on the stems of recent species of *Cycas*, but as SCHENK also suggested, the scales may be compared with the expanded bud-scales of a recent *Agathis* shoot. SCHENK has described the structure of the epidermis of some German Rhætic species of *Podozamites*, adding that the form of the cells does not favour an alliance with *Agathis*: his drawings do not appear to us to warrant this inference.

A comparison between the leaves of *Podozamites* and those of existing species of *Agathis* seems to us suggestive of affinity, and without venturing to speak with confidence in the absence of more satisfactory evidence than is at present forthcoming, we are inclined to think that some, at least, of the numerous and widely spread species of BRAUN's genus may be Mesozoic representatives of the Araucarieæ.

Good examples of *Podozamites* have been figured by many authors; for purposes of comparison with *Agathis* reference may be made to the sources mentioned in the footnote.\*

In this short summary of the evidence bearing on the past history of the Araucarieæ, we have not attempted to give a complete list of recorded species, many of which are worthless, but we have cited such records as may serve to illustrate both the nature of the available documents and the wide distribution and comparative abundance of Araucarian plants—more particularly during the Mesozoic era. A critical revision of the published lists of fossil Conifers is much needed; GOTHAN's recent work† goes some way towards demonstrating the need of caution in attaching significance to the generic terms *Araucarites* and *Araucarioxylon* which occur in palæobotanical literature in a profusion, which serves to demonstrate a lack of scientific restraint on the part of authors rather than to illustrate the abundance of joint Araucarieæ. We believe that further research will strengthen the view that palæontological records point to the Araucarieæ as superior in antiquity and relative importance to the Abietineæ. The Rhætic fossils from Scania, described by NATHORST‡ as species of *Pinites*, may be referable to the Abietineæ, but the very imperfect cones and winged seeds which he figures do not afford convincing testimony as to the existence of Pinus-like plants in the Rhætic vegetation. If the Abietineæ played a more important rôle in the older Mesozoic floras than the Araucarieæ, we should expect to find a greater abundance of their vegetative shoots and cones in the Jurassic and Rhætic rocks. The present distribution of the Araucarieæ as compared with that of the Abietineæ appears to us indicative of the greater antiquity of the former, and this suggestion is consistent with palæobotanical data.

\* BRAUN (1843), SCHENK (1867), SEWARD (1900, 1904), GEYLER (1877), YOKOYAMA (1889), VELENOVSKY (1885).

† GOTHAN (1905).

‡ NATHORST (1876), p. 31, Plates 14–16.

## XI. PHYLOGENETIC CONSIDERATIONS AND CONCLUSION.

*Nicht die Descendenz ist es, welche in der Morphologie entscheidet, sondern umgekehrt die Morphologie hat über die Möglichkeit der Descendenz zu entscheiden (BRAUN).*

Professor COULTER's\* opening sentences in his paper on "The Origin of Gymnosperms and the Seed Habit" may serve as a fitting introduction to the following considerations :—

"The most difficult as well as the most fascinating problem in connection with any group is its phylogeny. The data upon which we base opinions concerning phylogeny are never sufficient, but such opinions usually stimulate research and are necessary to progress."

In a paper worthy of the author, BRAUN,† in 1875, drew attention to the gulf between Phanerogams and Cryptogams, a gulf which is crossed neither by existing nor extinct plants. He pointed out that the Cycadaceæ exhibit certain features which afford an indication of possible lines of affinity between the Filicales and Gymnosperms.

Since 1875 considerable progress has been made in our efforts to discover the probable links connecting Pteridophytes and Gymnosperms. The work of the Japanese botanists—IKENO and HIRASE—stands out as one of the most valuable contributions, so far as existing plants are concerned, in this connection, but it is from the results of researches into the morphology of plants which have ceased to exist that it has been possible to construct some of the branches of the genealogical tree of the Gymnosperms. Palæobotanical investigations have at least demonstrated the danger of accepting class distinctions, well established by long usage, as representing impassable barriers between the Vascular Cryptogams and Seed-bearing plants.

We have endeavoured to show that the Araucarian type is one of the oldest if not the oldest of the Coniferales. This conclusion, though opposed to views expressed by Professor JEFFREY‡ and Mr. THOMSON,§ is one which we believe to be in accord with palæobotanical evidence. It requires but a slight acquaintance with existing plants to demonstrate the fallacy that primitive characters and geological antiquity are necessarily associated. On the other hand, if we have evidence that the Araucarieæ are older than the Abietineæ—that the former in the early stages of the Mesozoic era had a distribution and a relative predominance in contemporary vegetation comparable with that of the Abietineæ to-day—we may reasonably expect to find that the morphological characters of the older group are simpler and less specialised than those of the newer group.

\* COULTER (1898), p. 1.

† BRAUN (1875), p. 267.

‡ JEFFREY (1905), p. 33.

§ THOMSON (1905), p. 54.

The comparison of the Araucarieæ and Cordaitales, which is instituted in a later page, makes reference to most of the anatomical characteristics of the vegetative organs of *Araucaria* and *Agathis*. There are, however, a few features worthy of notice bearing on the general question of the position of the Araucarieæ. The persistent character of the leaf-trace is a character which we are disposed to regard as primitive; it is an example of the retention of structures no longer essential to the living tree, a character which may be regarded as inconsistent with a more highly specialised and more delicately adjusted type. The homogeneous structure of Araucarian wood—without resin-canals and xylem-parenchyma—is another character in keeping with a more primitive organisation. The secretion of resin occurs, but in place of special cells or canals we find water-conducting elements assuming a function other than that for which they are primarily adapted.

STRASBURGER\* has shown that in the Araucarieæ, as in the Taxineæ, albuminous cells occur as phloem-parenchyma only, and not as constituents of the medullary rays, a character which he considers denotes a more primitive structural type.

The apical cone of the Araucarieæ is characterised by a simplicity of structure which may be compared with that of *Lycopodium*; the value of the apex as an index of descent is no doubt small, but the anatomical characters are undoubtedly in closer agreement with those of the Lycopods than with those of the Ferns.

It is not with the Gymnosperms as a whole that we are chiefly concerned, but with a section of the Coniferales.

The Cycads must of necessity receive a passing notice, as we cannot entirely dissociate the Coniferales and Cycadales in speculating on the ancestry of one or other of the two groups. Since the date of BRAUN's paper abundant evidence has been brought to light amply justifying the generally accepted view that modern Cycads are descendants of extinct types which had their origin in fern-like ancestors. Recent Ferns and Cycads exhibit features in common, but from the records of the Palæozoic era in particular it has been possible to demonstrate that these resemblances are signs of community of descent. It is not our intention to discuss the precise lines of evolution of the Cycads, but we are disposed to regard the Medulloseæ as stages in the development of Cycadean plants.† Granting the filicinean origin of the Cycadaceæ, can we also link on the Coniferales to this line of evolution, or is there a preponderance of evidence in favour of the view, not infrequently expressed, that it is the Lycopodiaceous phylum which affords a more promising starting-point for the roots of the Conifer stock?

Among extinct plants which have a direct bearing on the question of the mono-

\* STRASBURGER (1891), p. 92.

† In reference to this subject, in addition to the writings of SCOTT, WORSDELL, and others, see also MATTE (1904). Since this was written, a paper has been written by Mr. WORSDELL ('Annals of Botany,' vol. 20, p. 129, 1906), in which he gives a *résumé* of his views on the origin of Cycads from Pteridosperms.

phyletic or polyphyletic origin of Gymnosperms, the genus *Cordaitea* is one of the most important. The late M. RENAULT,\* of Paris, whose researches enable us to regard this Palæozoic genus almost in the light of a living plant, recognised that it exhibits points of contact with Cycads, Conifers, *Ginkgo*, and the Gnetales. This generalised type may be regarded, therefore, as affording some support to the monophyletic origin of Conifers (or at least the Araucarieæ) and Cycads. Before referring to other types suggestive of a combination of Cycadean and Coniferous characters, we must briefly assess the value of the evidence on which *Cordaitea* has been compared with the Araucarieæ.

The structure of the wood is practically identical with that of *Agathis* and *Araucaria*. PENHALLOW,† in a recently published work of considerable importance, discusses the anatomical resemblance between *Cordaitea* and the Araucarieæ; he concludes that both *Agathis* and *Araucaria*, the latter a relatively higher type than the former,‡ are derived from *Cordaitea*. He regards his observations, which are solely anatomical, as confirmatory “in a very striking manner of the probable monophyletic origin of Gymnosperms as already expressed by COULTER.”†

The chief resemblances between *Cordaitea* and the Araucarieæ are—(i) The presence of polygonal bordered pits on the tracheal walls; (ii) a comparatively wide transition zone between the spiral protoxylem elements and the normal type of secondary wood; (iii) the form of leaf and the habit of the vegetative shoots in *Cordaitea* and *Agathis*.

(i) and (ii) We recognise the obvious agreement between the secondary xylem of *Cordaitea* and that of the Araucarieæ, but this may be expressed by the statement that this particular type of tracheal tissue is known to be of common occurrence among Palæozoic plants, and probably represents a more primitive design of conducting tissue than that of the recent genera of Coniferales. In view of this consideration, and more especially in face of the fact that the less plastic reproductive organs of *Cordaitea* are far removed from those of the Araucarieæ, we incline to the view that PENHALLOW and others have over-estimated the significance of the anatomical similarity between the wood of the Palæozoic tree with that of the Araucarieæ.

(iii) The resemblance between the leaves of *Cordaitea* to those of *Agathis* and, it may be added, to a slightly less extent to certain species of *Podocarpus* (Sect. : NAGEIA) is fairly close as regards external form, but an anatomical comparison reveals a much less close correspondence. In the vascular bundle of the leaf of *Cordaitea* the protoxylem is on that side of the xylem next the phloem, as in Cycadean leaf-bundles; in some species of *Cordaitea*, as in Cycads, the xylem is mesarch, consisting of both centripetal and centrifugal tracheids, but according

\* RENAULT (1879).

† PENHALLOW (1904), p. 270.

‡ PENHALLOW (1904), p. 720. See also COULTER (1898).

to a recent communication\* most of the species of *Cordaite*s have no centrifugal xylem. The presence of a bundle-sheath (two to three cell-layers) encircling the veins of fossil leaves is another character—probably of little importance—which is unrepresented in *Agathis*. It is possible, however, that the transfusion tracheids which form a prominent feature in *Araucaria* are homologous with the conducting centripetal xylem of *Cordaite*s, but in *Agathis* this tissue is very feebly developed.

Whether or not WORSDELL† and BERNARD‡ are correct in their view as to the morphological value of the transfusion tissue, it is clear that the correspondence between the leaves of the fossil and of the recent genus—more especially in regard to the vascular tissue, but also as regards the mesophyll generally—is not sufficiently intimate to serve as a valid reason for assuming close relationship.

The abundance of transfusion tissue in the leaves of *Araucaria* cannot be regarded as a feature peculiar to the genus; the bundles in the leaves of *Sequoia* and other conifers are similarly provided with these tracheal elements. It is possible to regard the well-developed centripetal xylem of *Araucaria* as an argument in favour of the view that Cycads and Conifers are derivatives of an ancient filicinean stock. Although there is much to be said in favour of the opinion of WORSDELL and BERNARD that the transfusion tissue is homologous with the centripetal xylem of Cycads, we are far from admitting that their interpretation binds us to see in the transfusion tissue of *Araucaria* a Cycadean feature. The large isodiametric tracheids, which gradually increase in abundance towards the tip of the leaf and finally replace the centrifugal elements, may serve the purpose of water storage, and in function and origin may be compared with the water reservoirs described by HEINRICHER§ in dicotyledonous leaves. Moreover, the leaves of *Lepidodendron* are similarly well provided with almost identical elements, and we fail to see any adequate reason for assigning to them a phylogenetic significance.

The leaf-traces of *Cordaite*s are characterised by consisting of two equal bundles both in their course through the cortex and at their junction with the wood of the stem. As WILLIAMSON|| pointed out, in this feature *Cordaite*s and *Ginkgo* agree, an agreement which extends to other characters¶ of greater importance; in the *Araucarieæ*, on the other hand, the leaf-traces join the xylem of the stem as single bundles.

The reproductive organs of *Cordaite*s are of a type *sui generis*, and cannot be closely correlated with any existing genus. The male flowers may be best compared with those of *Ephedra*, *Gnetum*, and *Ginkgo*; the seeds recall those of Cycads and

\* STOPES (1903).

† WORSDELL (1895).

‡ BERNARD (1904).

§ HEINRICHER (1885).

|| WILLIAMSON (1877).

¶ SEWARD and GOWAN (1900).



*Ginkgo*, but the morphology of the female flowers does not suggest any close relation to other types, either recent or extinct. It has, however, been pointed out\* that the morphology of the inflorescence may be brought into line with that of the Abietineous cone if the latter be interpreted in accordance with the axillary-branch theory of the ovuliferous scale. Assuming for the sake of argument that a parallelism exists between the inflorescence of the fossil genus and the cone of the Abietineæ, we do not admit that the older Araucarian type comes under the same category. We adopt the view that the cone-scales of *Agathis* and *Araucaria* are carpellary leaves, and as such are poles-asunder from the flowers of *Cordaites*.

The combination in *Cordaites* of characters pointing to Cycadean and Coniferous affinity is not in itself a strong argument in favour of the common origin of the two groups. Additional data bearing on the position of *Cordaites* and its connection with other plant groups have, however, been furnished by Scott.† Certain stems from Lower Carboniferous rocks (e.g., *Calamopitys fascicularis* and *Dadoxylon Spencersi*, SCOTT), possess secondary wood of the Cordaitean type, but with the addition of several strands of primary xylem, occupying a more or less peripheral position in the pith; another stem described by the same author, characterised by similar primary strands, possesses secondary wood with broader medullary rays like that of Cycads and various genera of Cycadofilices. The primary strands of these stems agree in their mesarch structure with those of *Lyginodendron* and *Heterangium* and constitute a connecting link between these Lower Carboniferous stems on the one hand and the Cycads and Cycadofilices on the other. It would be interesting to know what kind of reproductive organs were borne on the stems; possibly the seeds were of the highly specialised type, which is now known to have characterised certain Palæozoic plants for which the appropriate term Pteridospermæ‡ has been employed. If we consider the vegetative stems alone, a limitation imposed by lack of knowledge, their anatomy undoubtedly constitutes an argument of importance in favour of SCOTT's conclusion that the Cordaites-phylum included certain generic types exhibiting anatomical characteristics which bring them into line with a Cycad-fern stock. If we adopt this view, and we are not questioning its soundness, how far does it affect the connection between the Araucarian and the Cycadofilicean phyla? We have again to decide whether the Cordaites-phylum—admitting that we may legitimately include under this head such genera as *Calamopitys*, *Pitys* and *Dadoxylon*—is sufficiently closely related to the Araucarieæ to be allowed the weight of a determining factor in deciding for or against the Filicinean ancestry of that section of the Coniferales, of which *Agathis* and *Araucaria* alone survive. As we have already stated, we hold the view that *Cordaites* differs too much from the Araucarieæ to be regarded as a decisive criterion in reference to the phylogeny of the latter.

\* SCOTT (1900), p. 436.

† SCOTT (1902).

‡ OLIVER and SCOTT (1904); ZEILLER (1905).

We will now consider the Araucariæ from the point of view of their possible derivation from ancestors which were rather Lycopodiaceous than Filicinean. We are aware that it has been recently stated by Jeffrey that it seems impossible to refer the Coniferales any longer to a Lycopodinous ancestry.\* This author deduces from a comparative study of the fibro-vascular skeleton of plants that the Lycopods are distinguished by the absence of foliar gaps in the central cylinder from the Filicales and Phanerogams; a difference to which he assigns a considerable importance from the standpoint of phylogeny. He divides the vascular plants into Lycopsidea and Pteropsida; the former comprising the Lycopodiales and Equisetales,† characterised by the ramular gaps in the central cylinder and by the absence of foliar gaps; the latter, including the Filicales, Gymnosperms and Angiosperms, distinguished by the presence of foliar gaps in addition to ramular gaps. The anatomical distinguishing features of these "two great primitive stocks" are interpreted as characterising two independent lines of evolution and constituting, therefore, a strong argument in favour of a Filicinean ancestry for Conifers as well as Cycads. We consider that the characters on which this twofold grouping is based are estimated at too high a value as indices of affinity. Granting the value of anatomy in phylogenetic considerations, we cannot concede to the structural plan of vegetative organs so preponderating an importance as is assigned to it by JEFFREY. SCOTT‡ also holds the view that both Cycads and Conifers are derived from Filicinean ancestors. OLIVER§ has expressed the same opinion; in reference to *Lepidocarpon*, this author writes: "But in view of the probable Filicinean affinities of the Cycads and of the other Gymnosperms, *Lepidocarpon* is only of value for the moment as an analogy." In another place OLIVER says: "It may, however, be observed with some confidence, that the *Lepidocarpon* type left no seed-bearing progeny."|| We prefer to attach to *Lepidocarpon* considerable importance as an extinct type presenting a close homology in its sporophylls with the ovuliferous scales of the Araucariæ and to regard it as a possible connecting link between the Araucariæ and Lycopods. We are disposed to think that the proved relationship between Cycads and Ferns has been allowed an undue influence on opinion regarding the ancestry of the Conifers. The view expressed by several botanists that it is among the Lycopodiaceous plants that the ancestors of the Conifers may be found has been recently stated by CAMPBELL,¶ who says: "The Gymnosperms (at least the Conifers) are probably direct descendants of some group of Lycopods allied to the Selaginellaceæ, or Lepidodendriaceæ, while the origin of the Cycads and Angiosperms is to be looked for among

\* JEFFREY (1905).

† *Ibid.* See also JEFFREY (1900).

‡ SCOTT (1900).

§ OLIVER (1904).

|| OLIVER (1903).

¶ CAMPBELL (1905), p. 606. See also POTONIÉ (1899), p. 321; (1902), p. 753.

the Eusporangiate Filicinæ." Our contention is that this opinion as to the ancestry of the Coniferales, or at least the Araucarieæ, is one which deserves more attention than it has recently received and, in the present state of our knowledge, it is the view which appears to us the more probable. In the first place it is essential to form an opinion as to the position of the Araucarieæ within the Coniferales; we shall not attempt, at least in this communication, a revision of the grouping of the whole of this somewhat heterogeneous section of the Gymnosperms, but restrict ourselves to one definite point, are the Araucarieæ primitive in comparison with other Conifers? That they are among the oldest members of this group may be taken as an established fact, and we go a step further in believing that they bear the impress of plants of a comparatively low or primitive type.

Some of the features which we regard as supporting this view have already been mentioned, but we will now briefly consider the morphology of the reproductive shoots as a test of the primitive character of the Araucarieæ.

In a monograph on the male flowers of Gymnosperms, THIBOUT\* states that those of Araucarieæ exhibit points in common with the flowers of Cycads. In the structure of the sporophylls and in the arrangement of the vascular tissue THIBOUT considers that the Araucarieæ, more than any other Conifers, resemble the Cycadaceæ. But we are disposed to take the view that the male flowers of Cycads and Conifers are not constructed on a sufficiently similar plan to render easy a close comparison. The microsporangia of the former exhibit features which bring them fairly close to the sori of ferns, a fact brought out by WARMING, TREUB, LANG† and other botanists and confirmed by the recent investigations of WIELAND‡ into the male flowers of *Bennettites*. In the Coniferae, on the other hand, the sporophylls belong to a distinct category; the great majority of genera have stamens of a fairly uniform pattern, but *Agathis* and *Araucaria* stand apart in having long, free and more numerous microsporangia recalling the sporangia of *Equisetum*. The male strobilus of the Araucarieæ, at least that of *Araucaria*, is characterised also by its large size and greater similarity in this respect to the female shoot, and in the gradual transition from foliage leaves to sporophylls.

We do not wish to lay undue stress on the external resemblance of the male flowers in some species of *Araucaria* (e.g., *A. Bidwillii*) to the strobili of certain existing Lycopods and to the Palæozoic Lepidostrobi; but can we recognise resemblances of greater significance?

As regards the resemblance between *Equisetum* and the Araucarieæ; the genus *Cheirostrobis*§ exhibits an interesting association of Equisetaceous and Lycopodiaceous features in combination with others bringing it into relationship with *Sphenophyllum*.

\* THIBOUT (1896).

† WARMING (1879); TREUB (1884); LANG (1897).

‡ WIELAND (1899, 1899<sup>2</sup>); COULTER and CHAMBERLAIN (1901), p. 142.

§ SCOTT (1897).

In the words of the author of the genus, "*Cheirostrobus* combines in a striking manner the characters of three of the main divisions of Pteridophytes; the Equisetineæ, the Lycopodineæ, and the Sphenophylleæ."\* As regards the Lycopodiaceous strobilus; in *Lepidostrobus* we meet with heterosporous cones in which the microsporangia, like the megasporangia, occur as elongated sacs on the upper face of the sporophyll with a ligule intervening between the distal end of the sporangium and that of the sporophyll. In *Araucaria* the microsporangia are not on the upper face of the sporophyll nor is a ligule present, distinguishing features which it is difficult to estimate at their true value. The form of the sporangia in the two types is not dissimilar and the difference in their number and position need not constitute a fatal bar to relationship. But in *Cheirostrobus*, one of those generalised types which serve as finger-posts to the paths which evolution has followed, we have a genus which serves, in some measure, to bridge over the gap between the male sporophylls of the Araucarieæ and those of Lycopodiales.

The microspores of the Araucarieæ have not been fully investigated, but in a recent paper LOPRIORE† has described those of *Araucaria Bidwillii* and his observations confirm those of THOMSON‡ as to the existence of numerous nuclei in the pollen-tubes of some at least of the Araucarieæ. LOPRIORE found as many as 44 nuclei in the tubes of *A. Bidwillii*; his figures of the microspores show the interior occupied by several cells with distinct walls and he describes the nuclear divisions which take place during the production of this tissue from the primordial nucleus of the spore. It would seem, therefore, that in the structure of the mature microspore *Araucaria* exhibits another and notable peculiarity among recent Gymnosperms. An obvious comparison which LOPRIORE makes is with the pollen-grains of *Cordaites*,§ but we may recognise in this character, exhibited both by the Palæozoic and recent Gymnosperms, a closer approach to Pteridophytic ancestors. We do not, however, admit that a simple type of male prothallus such as occurs in *Sequoia*, *Taxodium* and *Torreya* necessarily constitutes an important criterion in estimating the relative positions of genera in a natural system of classification. If Conifers had their ancestry among Filicinean plants, we might reasonably expect to find in the more primitive and older genera a closer approach to a less highly specialised type of microspore. Miss ROBERTSON,|| in her valuable contribution to our knowledge of the genus *Torreya*, has referred to this point and, as a means of reconciling facts not in accord with reasonable expectation, she has suggested an explanation which is

\* SCOTT (1897), p. 22.

† LOPRIORE (1905). The structure of the microspores of the Araucarieæ will be dealt with by Mr. R. B. THOMSON in a forthcoming paper.

‡ In some preparations which Mr. THOMSON showed to one of us large pollen-tubes seen in sections of ovules appeared to be multinucleate, but it did not seem certain that the structures regarded as pollen-tubes might not be partially aborted megaspores. THOMSON's interpretation has now been fully justified.

§ OLIVER (1903).

|| ROBERTSON (1904).

ingenious if hardly convincing. She notices that the presence of cuticular bladders and of prothallial cells are associated characters; microspores with no prothallial cells, *e.g.*, those of *Taxodieæ*, *Cupresseæ* and *Taxeæ* have no bladders and are thus less well fitted for wind-dispersal. In the absence of the aid to dispersal afforded by a distended cuticle a maximum reduction of weight is desirable; it is suggested that the absence of prothallial cells may be interpreted as an adaptive character acquired for the sake of reducing the weight of the microspore to a minimum. The saving in weight must be so extremely small that one feels sceptical as to the adequacy of the hypothesis.

The pollen of *Cordaites*\* differ from those of most *Coniferales* in the greater number of cells which they contain, and so far as it is possible to draw a conclusion from such specimens as have been described, the arrangement of the gametophyte tissue appears to be on a plan different from that in any recent *Phaneorgam*. It is not difficult to institute a comparison between the gametophyte of such genera as *Isoetes* and *Selaginella* and the more reduced gametophyte in the Araucarian microspore, a reduction doubtless connected with the substitution of siphonogamous for zoidogamous fertilisation, which would demand as much space and material as possible for the production of the pollen-tube.

To pass to the female flower. The female flowers of the *Araucariæ* have already been briefly discussed from a morphological standpoint. It is clear from the occurrence of fairly well-preserved Jurassic cones and individual cone-scales and seeds that the present type of *Araucariæ*, especially that represented by the *Eutacta* section, is an old form, and we would add older than that characteristic of the *Abietinæ*. The comparison of the axillary female shoot of *Cordaites* with a single cone-scale of *Araucaria* or *Agathis*, constitutes the closest approach we can point to between the *Araucariæ* and any genus which may reasonably be regarded as a possible connecting link with the Cycad-Fern stock. This comparison is based on the assumption that the difference between the *Abietinæ*—in the narrower sense—and the *Araucariæ* is one of degree; it implies that the axillary-bud theory, if applied to the *Abietinæ*, is therefore the more probable explanation of the morphology of the Araucarian cone. The view that these two types must be brought into line involves us in needless difficulties; it means that the older and, as we think, the more primitive type has advanced further from its prototype than the more modern. According to our view the ovuliferous scale of an Araucarian cone is a single leaf modified for reproductive purposes and homologous with a foliage leaf. COULTER has pointed out that “one serious result of belief in the doctrine of types was the use of the more complex structures to explain the simpler ones, the reading of complexity into simplicity.”† This we consider applicable to the views of many botanists in regard to the morphology of the Araucarian cone-scale. The argument

\* RENAULT (1879); OLIVER (1904).

† COULTER (1904), p. 2.

in support of the axillary-bud theory in the case of *Pinus* and other genera receives considerable support from the occurrence of various grades of abnormalities in place of the normal ovuliferous scales, but in the Araucarieæ no such evidence is available, and the inference suggested is that the reproductive shoots of this section of the Coniferales are more stable and fixed.

We are, therefore, disposed to doubt the validity of the comparison between *Araucaria* and *Cordaites*. Moreover, the seeds of the latter differs considerably from those of the former. Can we, on the other hand, bring the Araucarian cone into closer touch with the strobili of recent or extinct Lycopods? With recent species of *Lycopodium* the Araucarieæ agree in having strobili consisting of spirally-disposed sporophylls, each with a single megasporangium,\* but in shape the *Lycopodium* sporangium differs from that of the Araucarieæ, a matter of secondary importance. A more fundamental distinction is the fact that in one case we have a naked sporangium and in the other a true seed. One of the many advances of first-rate importance which we owe to Dr. SCOTT,† is the demonstration of the production of seed-like organs by an extinct Lycopodiaceous genus. The genus *Lepidocarpon* is peculiar in having advanced a stage beyond that of the other members of the Lycopodiales in the conversion by means of an outgrowth from the sporophyll of a naked megasporangium into an organ which, as SCOTT says, must be included in the category of seeds.

In discussing the affinities of *Lepidocarpon*, SCOTT writes: "Those who hold to the belief that the Gymnosperms, or a part of them, sprang from Lycopods, may find in the discovery of *Lepidocarpon* some support for their views."‡ If the integument of *Lepidocarpon*, instead of forming a slit-like micropyle, were closed over the top of the sporangium, leaving a fairly wide aperture near the proximal end, we should have an arrangement not unlike that in *Araucaria*, in which the sporophyll is wrapped round the integumented ovule, whereas in the fossil the sporophyll retains the form of an expanded bract and the integument alone serves as an enclosing envelope. The resemblance between *Lepidocarpon* and *Araucaria* extends also to the extension of the long and narrow nucellus into the micropyle, the presence of a columnar layer on the surface of the sporangium or nucellus, the absence of a pollen-chamber, and the presence of elongated cells in the middle of the prothallus. We regard *Lepidocarpon* as a very important link between the Araucarian seed and the normal Lycopodiaceous sporangium. There is another point to be considered, namely, the presence of a ligule in *Isoetes* and in *Selaginella* as in *Lepidocarpon* and *Lepidostrobus*. The membranous or awl-like outgrowth from the upper face of the Araucarian cone-scale has been compared with the ligule of

\* As GOEBEL says: "We should obtain the relationships of position of the female flower of *Dammara* rightly enough if we replaced by ovules the sporangia of a spike of *Lycopodium*." GOEBEL (1905), p. 521.

† SCOTT (1901), p. 324.

‡ *Ibid.* (1901).

recent Pteridophytes, but it is doubtful whether the employment of the term ligule in connection with cone-scales can be justified on grounds of morphological similarity.

We would also institute a comparison between the sporophyll of the Palæozoic Lycopodiaceous cone named by SCOTT *Spencerites*,\* and the cone-scale of *Agathis*. The former is distinguished by the absence of an integument; but in the form of the sporophyll and in the attachment of the sporangia by a narrow pedicel we notice a close resemblance to *Agathis*. Another feature of interest is a slight upward extension of the sporophyll tissue immediately beyond the sporangial stalk, which may be compared with the supposed representative of the ligule in an *Agathis* scale. A comparison of our fig. 24, E, with the diagram of *Spenceritis insignis* recently published by Miss BERRIDGE,† illustrates the similarity between the two types.

The structure of the ovule of the Araucarieæ, as we have already pointed out, differs from that of the majority of Conifers in certain respects; the protruded nucellus functioning as a stigma and the numerous and scattered archegonia are striking characteristics. In describing the archegonia of *Sequoia*, which, like those of *Araucaria* and *Agathis*, are irregularly placed in the prothallus, instead of occupying the customary apical position, ARNOLDI‡ has suggested that they constitute a primitive character.

The embryo of *Araucaria*, as described by STRASBURGER, possesses a peculiar feature in the occurrence of elongated cells at the top of the pro-embryo beyond the group of cells from which the young plant is ultimately produced. The significance of this feature, which is shared by *Cephalotaxus*, is by no means clear. If, as STRASBURGER§ suggests, the cells form a protective cap comparable with a root-cap, they may be considered as another sign of primitiveness. Another comparison has been made by a more recent writer between the pro-embryo of *Araucaria* and the protocorm of *Lycopodium*;|| a comparison which may be well founded, but which we do not feel is one to which much weight can be attached.

An obvious argument against the view which we advocate, namely, a relationship between the Lycopodiales and the Araucarieæ, is the difference between the vascular tissue. The comparison must clearly be made between the Araucarieæ and such Lycopodiaceous plants as possessed the power of secondary growth in thickness on a large scale. Both *Lepidodendron* and *Sigillaria* possess primary xylem which is clearly differentiated from the subsequently formed secondary wood. The primary xylem, as represented by such different types as *Lepidodendron vasculare*, *L. Harcourtii*, and *Sigillaria*, is centripetal in development, and may be regarded

\* SCOTT (1897<sup>2</sup>).

† BERRIDGE (1905), fig. 3.

‡ ARNOLDI (1900).

§ STRASBURGER (1879).

|| ARNOLDI (1900).

as corresponding to the xylem portion of the stele in *Psilotum*, a genus which retains in a very small degree the power of secondary growth.\*

Is there anything in the Araucariæ comparable with this? The transfusion tracheids, which form so prominent a feature in the leaves of *Araucaria*, are regarded by some botanists as homologous with the centripetal wood of Cycadean leaf-bundles. On this view it is possible to suppose that, as in recent Cycadean leaves, so also in the leaves of the Araucariæ, we have an ancestral feature which has disappeared from the vegetative stems. But we do not lay much stress on this hypothesis since it rests on the assumption, probable enough in itself, that the transfusion tracheids may be considered as centripetal xylem in a modified form. We agree with SCOTT† in the view which he has put forward, that the increasing power of forming secondary wood has led in the course of evolution to a gradual loss of centripetal conducting tissue, for the reason that such tissue becomes unnecessary, and even a source of inconvenience when there is an abundance of centrifugal xylem for purposes of transport. The differences between the Araucariæ and the Palæozoic Lycopods, so far as regards the primary xylem, may be accounted for as the result of anatomical changes consequent on a shifting of physiological processes during the course of evolution.

Another anatomical discrepancy between the two classes under consideration is the structure of the individual tracheids; in the Lycopods the xylem elements have scalariform pits, while the wood of the Araucariæ consists of tracheids with multiseriate bordered pits on the radial walls. As PENHALLOW‡ points out, instances of transition in the same plant, and even in the same tracheal element between scalariform and reticulate pitting are afforded by various plants, recent and extinct. The same author lays stress on the importance of the broad "transition-zone" in *Cordaites* as a primitive character in contrast to the more abrupt passage in higher types from the protoxylem elements to the normal secondary tracheids. The tracheids of the transition zone in *Cordaites* illustrate very clearly that the multiseriate hexagonal pits are but a modified form of the scalariform pits. A comparatively broad transition zone also characterises *Araucaria*. It would seem, then, that we have some justification for asserting that the two types of pitting—the Lycopodiaceous and the Araucarian—are not features which necessarily imply separate lines of descent.

As regards other anatomical features characteristic of Palæozoic Lycopods; the medullary rays are peculiar in consisting in great measure of slender, radially elongated elements with spiral and more or less reticulate pitting. PENHALLOW regards these tracheids as comparable with those in the rays of *Pinus* and *Tsuga*. This comparison, which has occurred to other botanists, would appear to lend support to the view that the genera which possess ray-tracheids are more primitive than the

\* BOODLE (1904).

† SCOTT (1902<sup>2</sup>).

‡ PENHALLOW (1904).



majority of Conifers in which no such elements occur. PENHALLOW, while holding that the Araucarieæ are more primitive than the Abietineæ, does not agree with those who derive Conifers from Lycopodiaceous progenitors; but he recognises the similarity in the medullary rays as one of more than superficial resemblance. He considers that, in response to certain conditions of growth and other causes, the older types of medullary ray have reappeared in certain less primitive members of the Coniferales. We believe that the absence of any elements in Araucarian wood of the same category as those in the medullary rays of *Lepidodendron* and *Sigillaria* may be connected with the well-marked differences between the primary xylem in the two sets of plants; the diminution in the primary xylem in the Araucarieæ has rendered superfluous radially conducting elements of tracheal form.

So far as we are able to judge, it would seem that in the *Lepidodendrea* the leaf-traces persist through secondary wood of considerable thickness, and in this we incline to recognise a point of agreement with the Araucarieæ.

The phloem of the Araucarieæ is not represented by any tissue of similar histological character in the *Lepidodendroid* stem, nor do we admit that anyone has so far demonstrated the existence of secondary tissue comparable with phloem in the Palæozoic Lycopods. Between the extra-cambial stelar tissues in the two sets of plants the differences are too great to render comparison possible.

Moreover, in *Lepidodendron* the method of secondary growth was of a peculiar type and is by no means satisfactorily explained; it was, at least, not identical with that in the Araucarieæ. It has been pointed out that in *Araucaria* there is a broad zone of unligified wood elements in the cambial region; this feature recalls the broad meristematic zone of the *Lepidodendrea*.\*

There are other obvious differences between the Lycopodiales and the Araucarieæ as regards the stem-anatomy, but we do not regard them as impassable barriers from the point of view of relationship.

PENHALLOW has shown that in the Araucarieæ there are no resin-parenchyma cells in the secondary wood; such resin as occurs being deposited in the cavities of ordinary tracheids. He suggests that the occurrence of resin-reservoirs in the fundamental tissues, cortex, and pith, is a legitimate inheritance from the mucilage canals of eusporangiate ferns, Cycadofilices, and Cordaites. We would supplement this statement by the addition of the *Lepidodendrea* as plants possessing secretory cell-groups or canals, which may be regarded as the precursors of the resin-passages in the Araucarieæ.

In the course of this account of the Araucarieæ we have endeavoured to emphasise the various characters in which the genera *Araucaria* and *Agathis* occupy a position apart among the Coniferales. In an exhaustive investigation on 'The Megaspore-membrane of the Gymnosperms,' Mr. R. B. THOMSON is led to regard the Araucariinae as occupying "a somewhat isolated position among the sub-groups of the Coniferales."

\* SEWARD and HILL (1900); SEWARD (1899).

This author, from the point of view of the characters which he examined also regards the Abietineæ as the most ancient group of the Coniferales.\* We cannot now extend our survey to the other families in this class, but we venture to suggest that the position of the Araucarieæ might be more clearly and accurately expressed by separating them from the other members of the group under the designation Araucariales, a subdivision of the Gymnosperms including the recent genera *Araucaria* and *Agathis* with such extinct types which there is good reason to believe are related to these survivals from the past. The great antiquity of the southern floras has long been recognised, and in citing the Cycads and the Araucarieæ as examples of survivals from the past, Sir WILLIAM THISELTON-DYER† expresses a fact which we believe to be amply supported by the testimony of the rocks. In the existing species of *Araucaria* and *Agathis*, we have remnants of a group of Gymnosperms which once flourished north of the Equator and occupied a position in the vegetation of the world from which they have been deposed by less ancient members of the Coniferales.

In conclusion we would point out that our position in relation to the question of the phylogeny of the Araucarieæ is that of advocates of a view which has received support in the past, but has of late hardly been accorded its due share of attention. Further discoveries among the extinct types preserved in Palæozoic rocks may prove us in the wrong; but if the arguments advanced are shown to be unequal to the task of supporting the hypothesis that some at least of the Conifers are not offshoots of a Filicinean stock, they may on the other hand do something to confirm the conclusions of those from whom, on the evidence before us, we are compelled to differ. We feel that the general consent which has deservedly been accorded to the view that the Cycadales and Filicales are intimately connected by descent, may have the effect of inducing an attitude too prone to overestimate the value of the arguments advanced in support of an extension of the idea of a Filicinean ancestry to other sections of the Gymnosperms.

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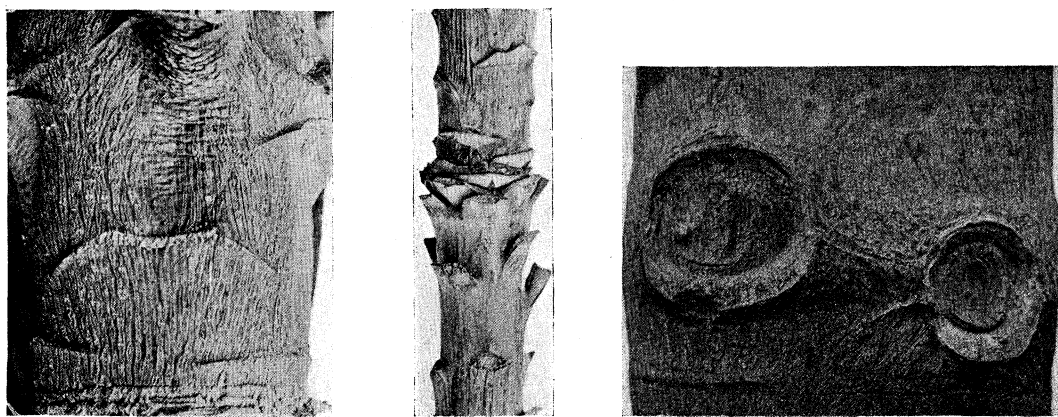
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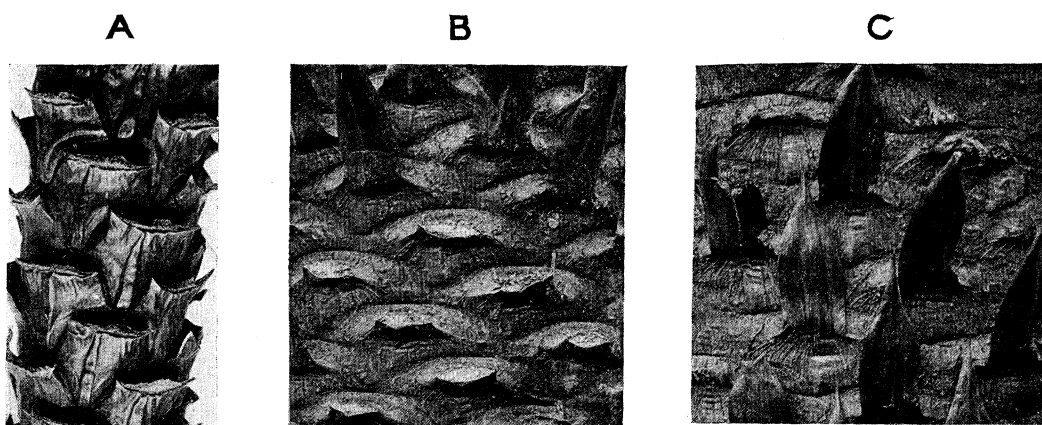


B

A

C

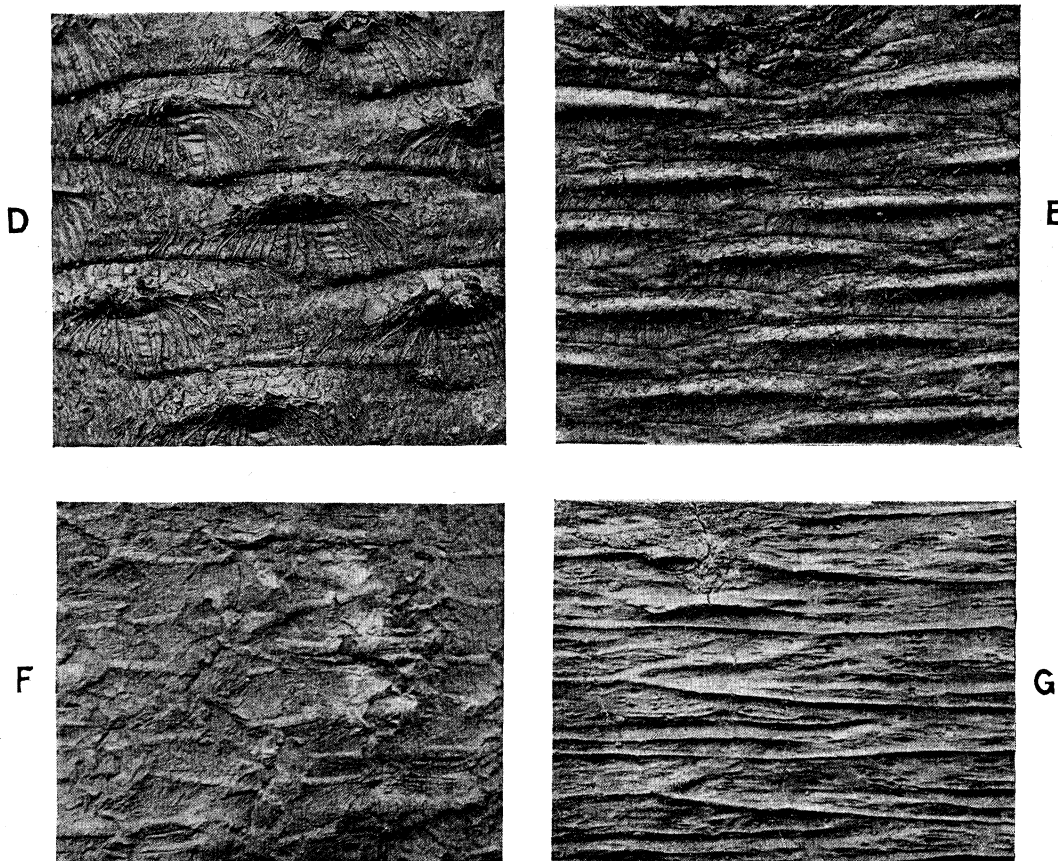
FIG. 2.—*Agathis robusta*.



A

B

C



D

E

F

G

FIG. 6.—*Arancaria imbricata*.



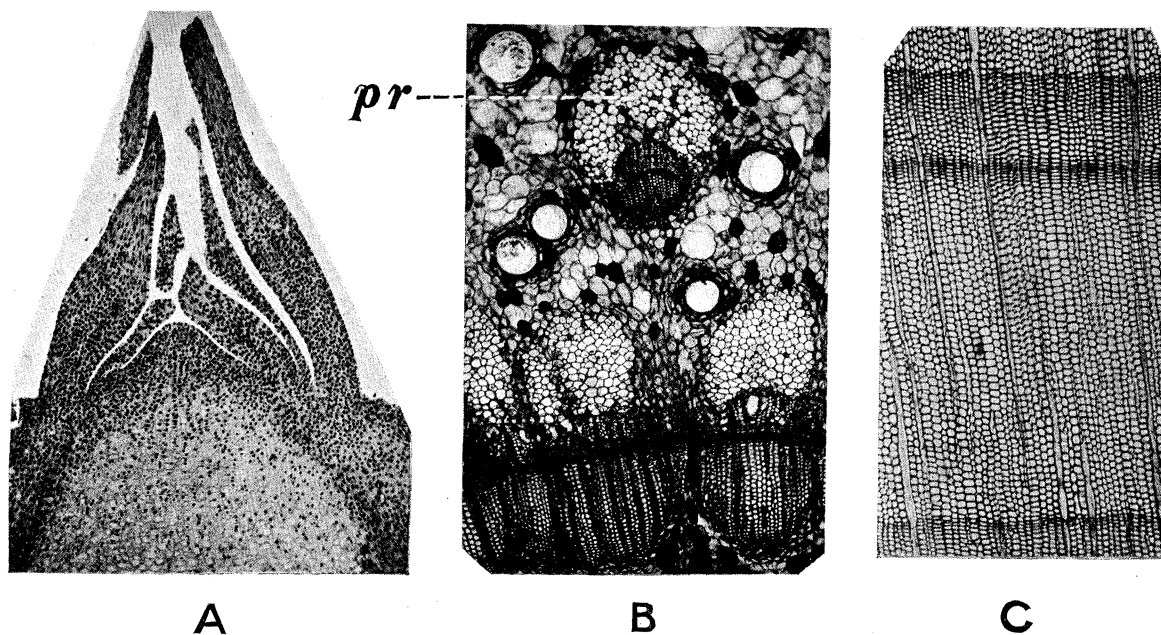


FIG. 17.—*Araucaria imbricata*.

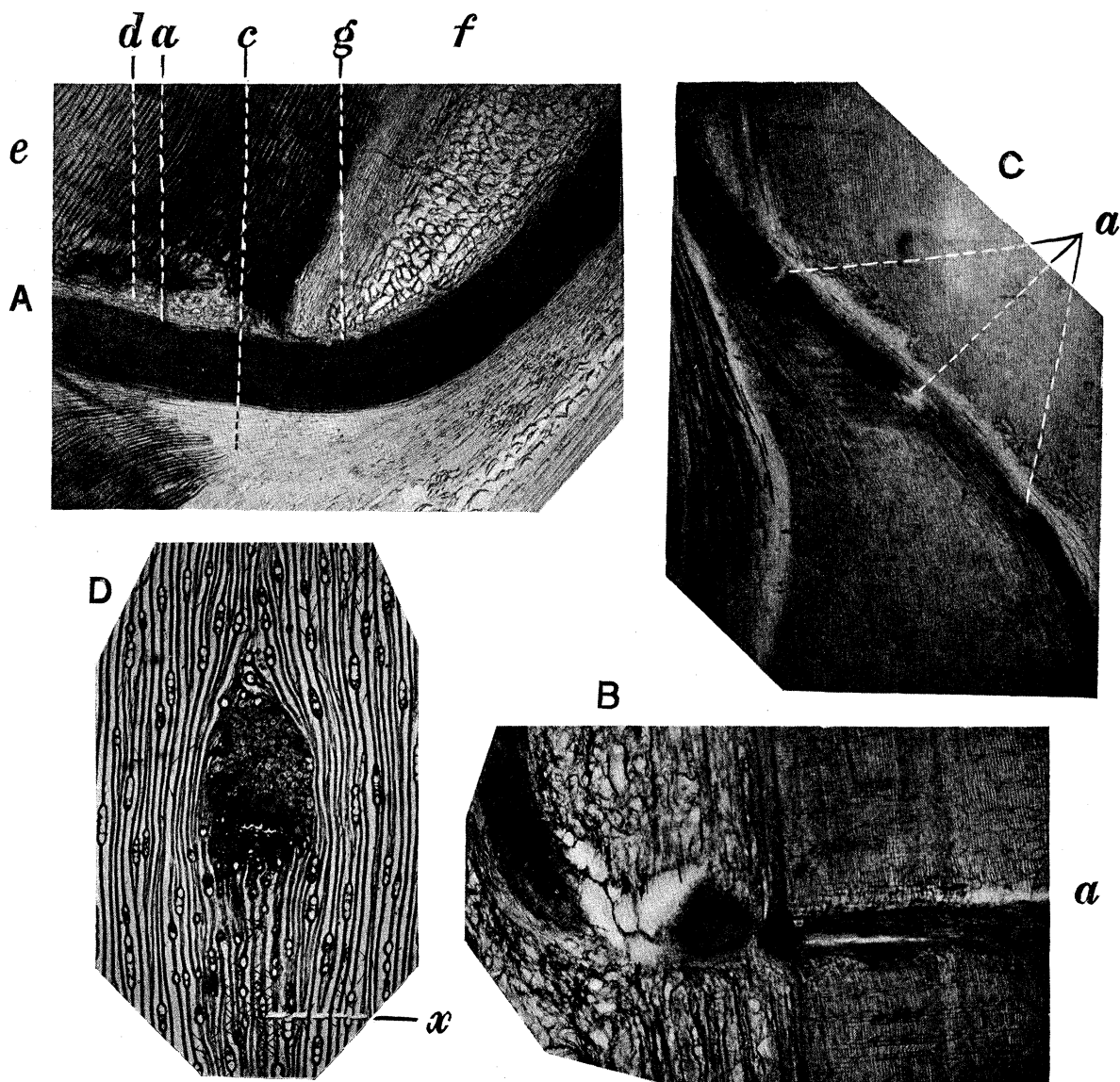
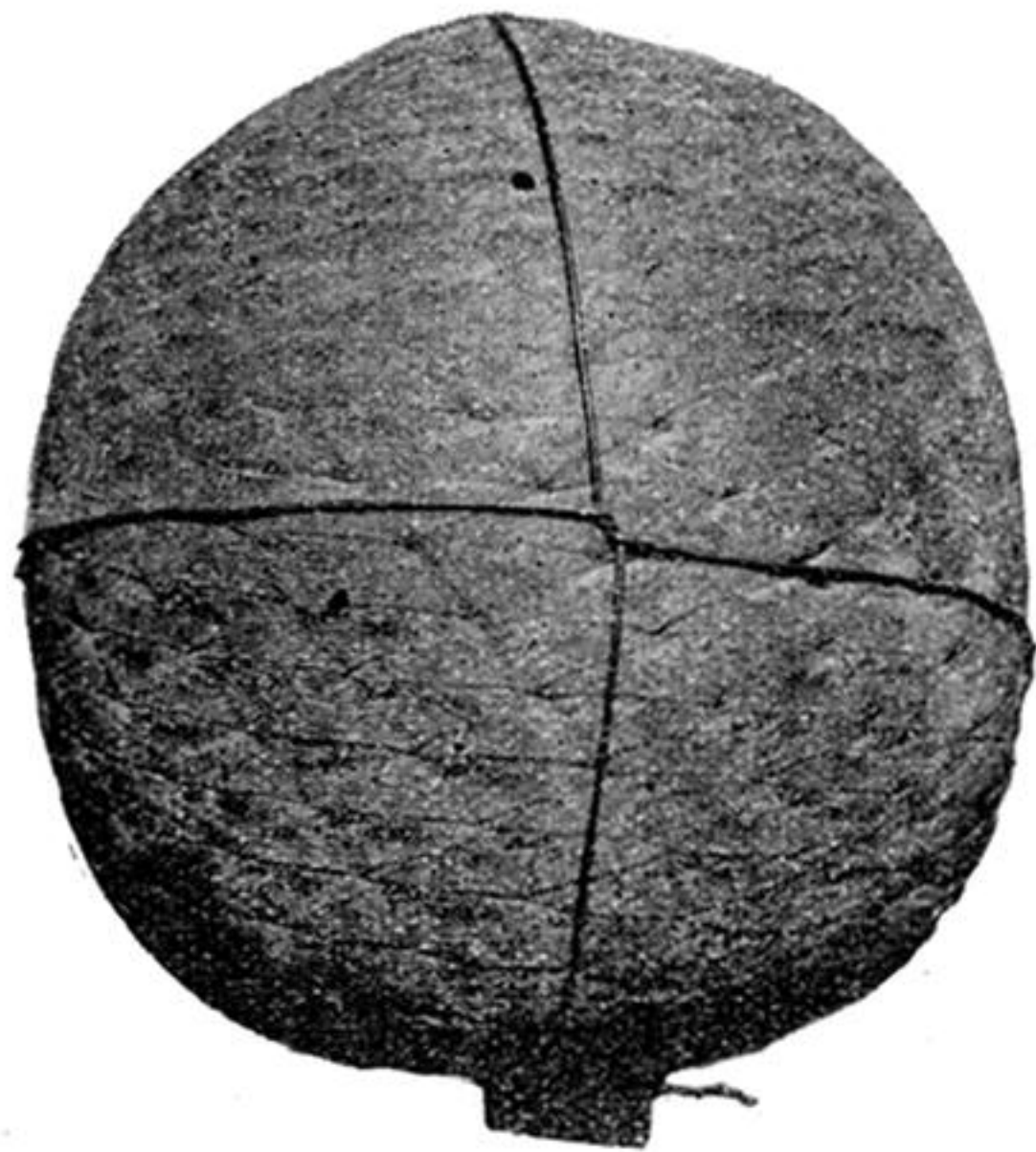


FIG. 21.—A, B, D, *Araucaria imbricata*. C, *Agathis robusta*.



A



B

FIG. 1.—Female Flowers. A, *Agathis Moorei* ( $\frac{1}{2}$  nat. size) ; B, *A. australis* ( $\frac{3}{4}$  nat. size).





FIG. 7.—*Araucaria imbricata*, in the EARL OF ANNESLEY'S Garden, Castlewella, co. Down.



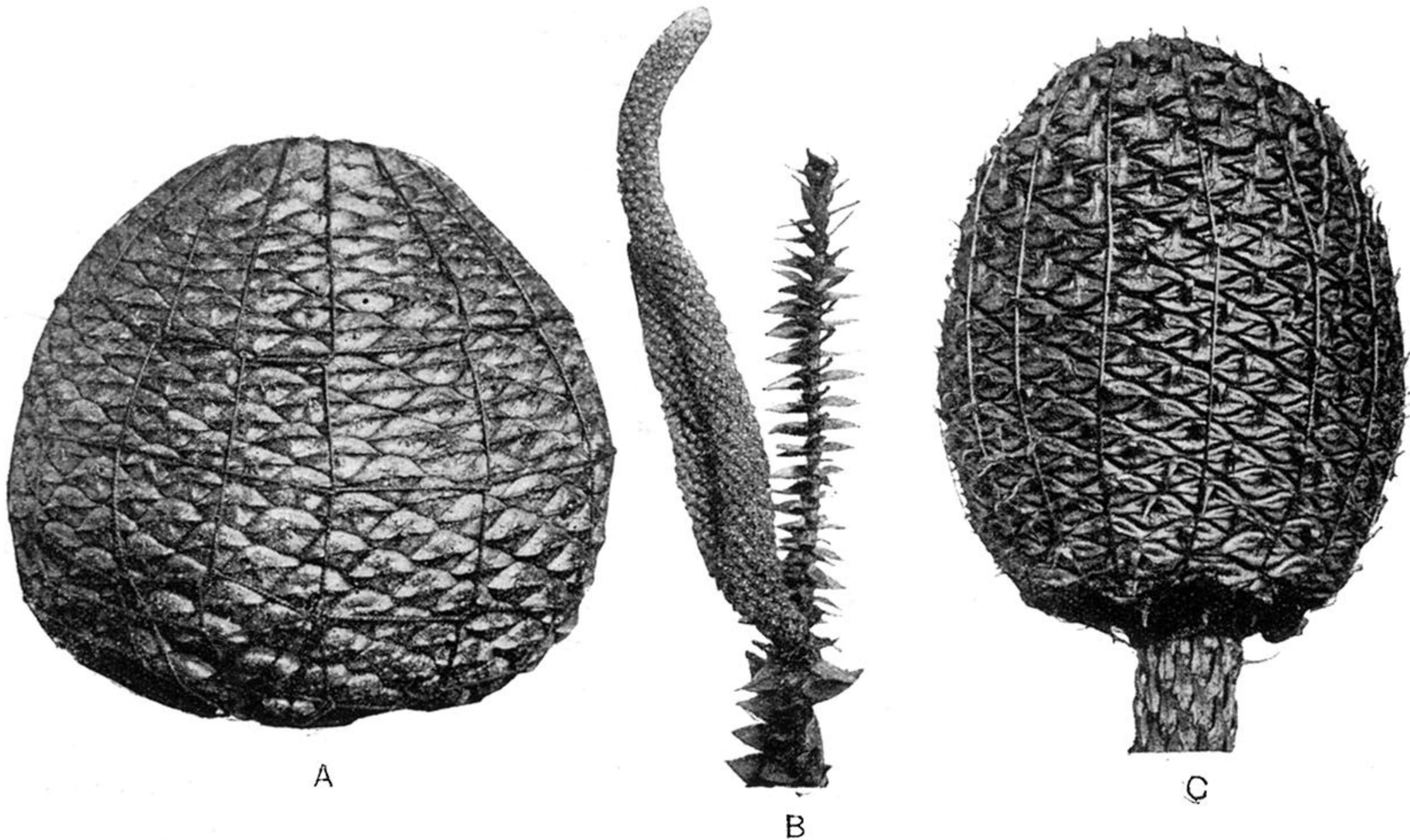


FIG. 8.—A, female flowers of *Araucaria brasiliensis*; B, Male flower of *A. Bidwillii*; C, Female flower of *A. Cunninghamii*.

(A,  $\frac{4}{9}$  nat. size; B,  $\frac{10}{27}$  nat. size; C,  $\frac{16}{21}$  nat. size.)



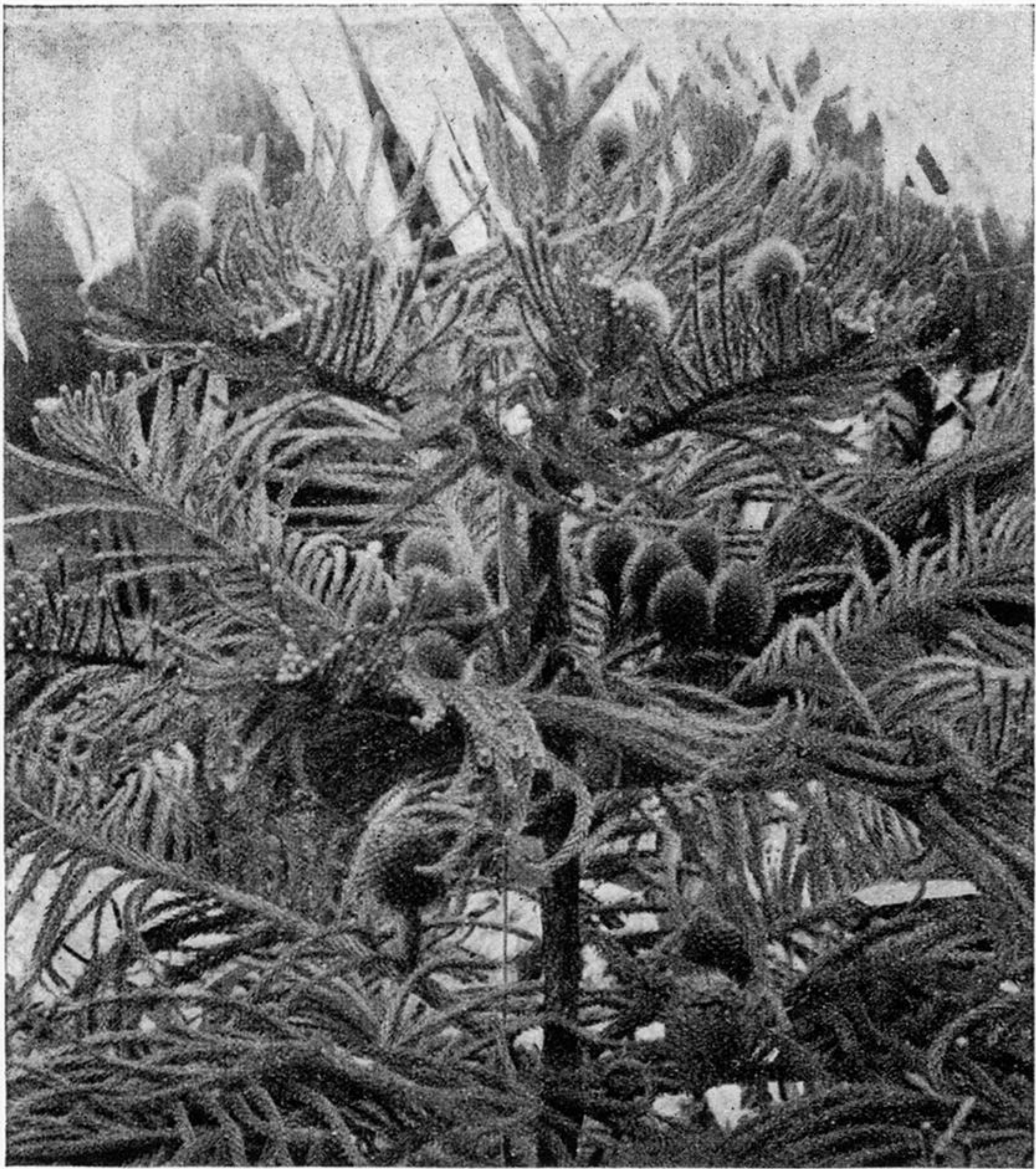


FIG. 12.—*Araucaria Cookii*, Cones in three stages of development.



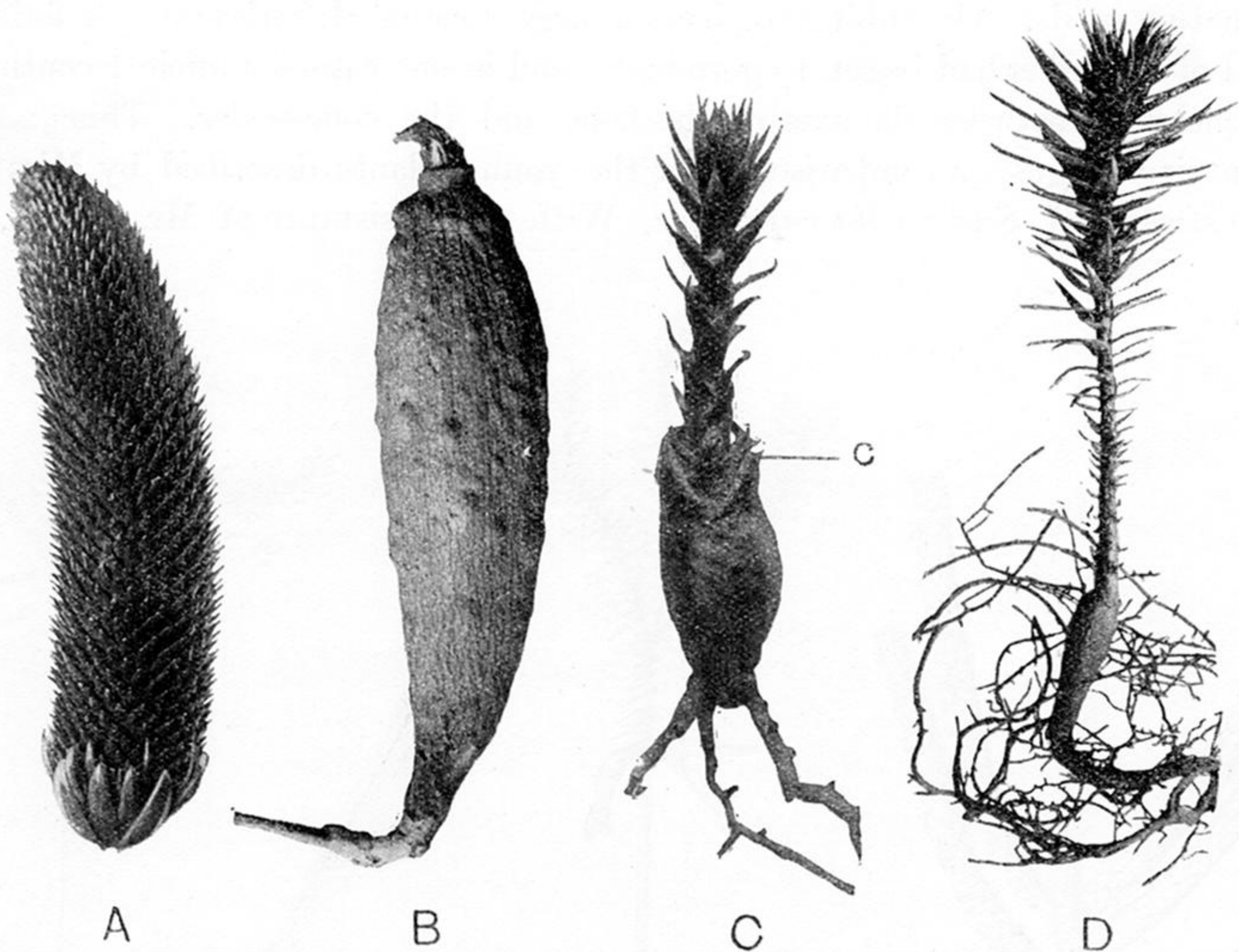


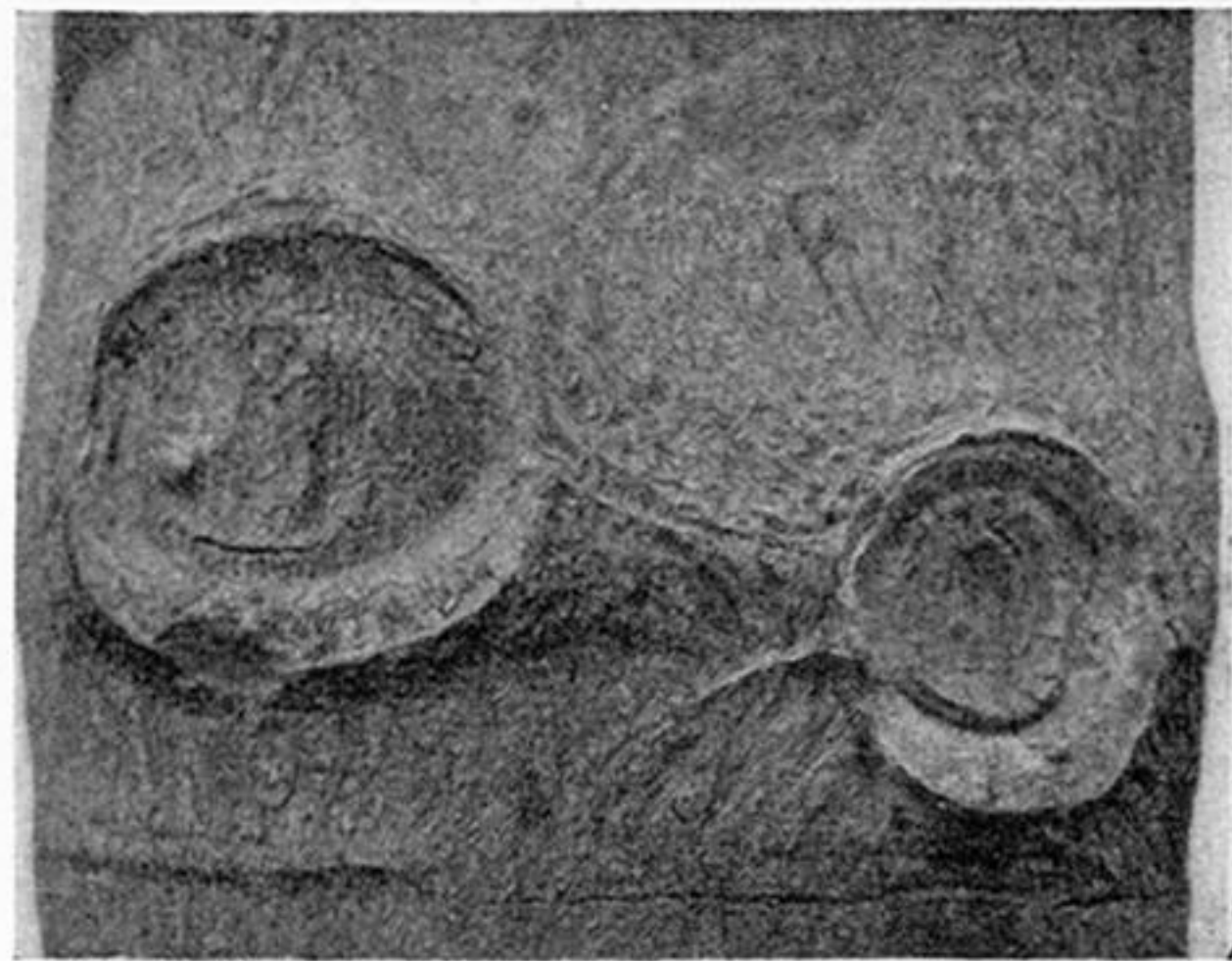
FIG. 13.—A, *Araucaria Rulei*, male flower ( $\frac{1}{2}$  nat. size) ; B, *A. Bidwillii*, seedling ; C, D, *A. imbricata*.  
(B—D nat. size.)



**B**



**A**



**C**

FIG. 2.—*Agathis robusta*.



A



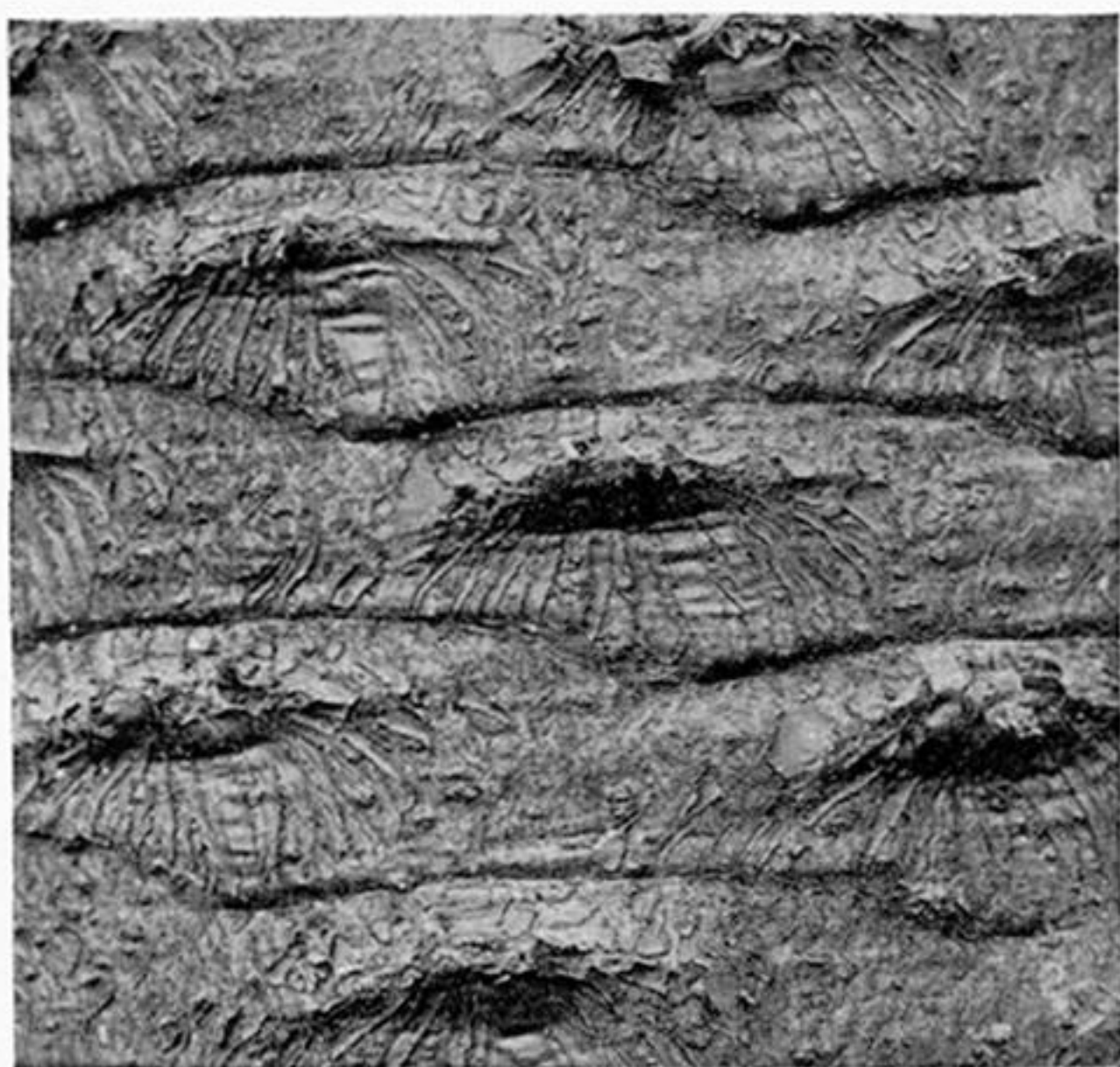
B



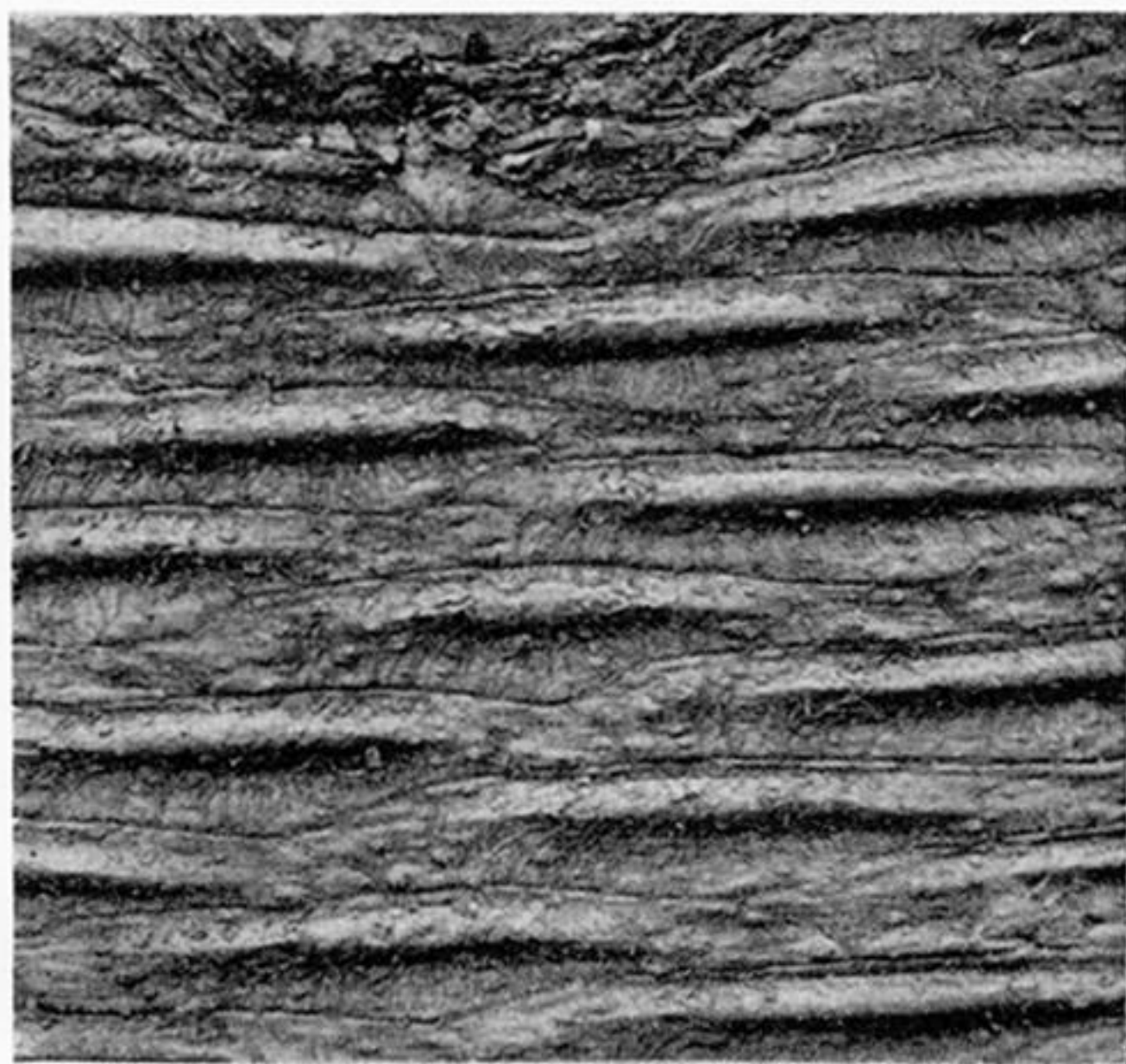
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E



F



G

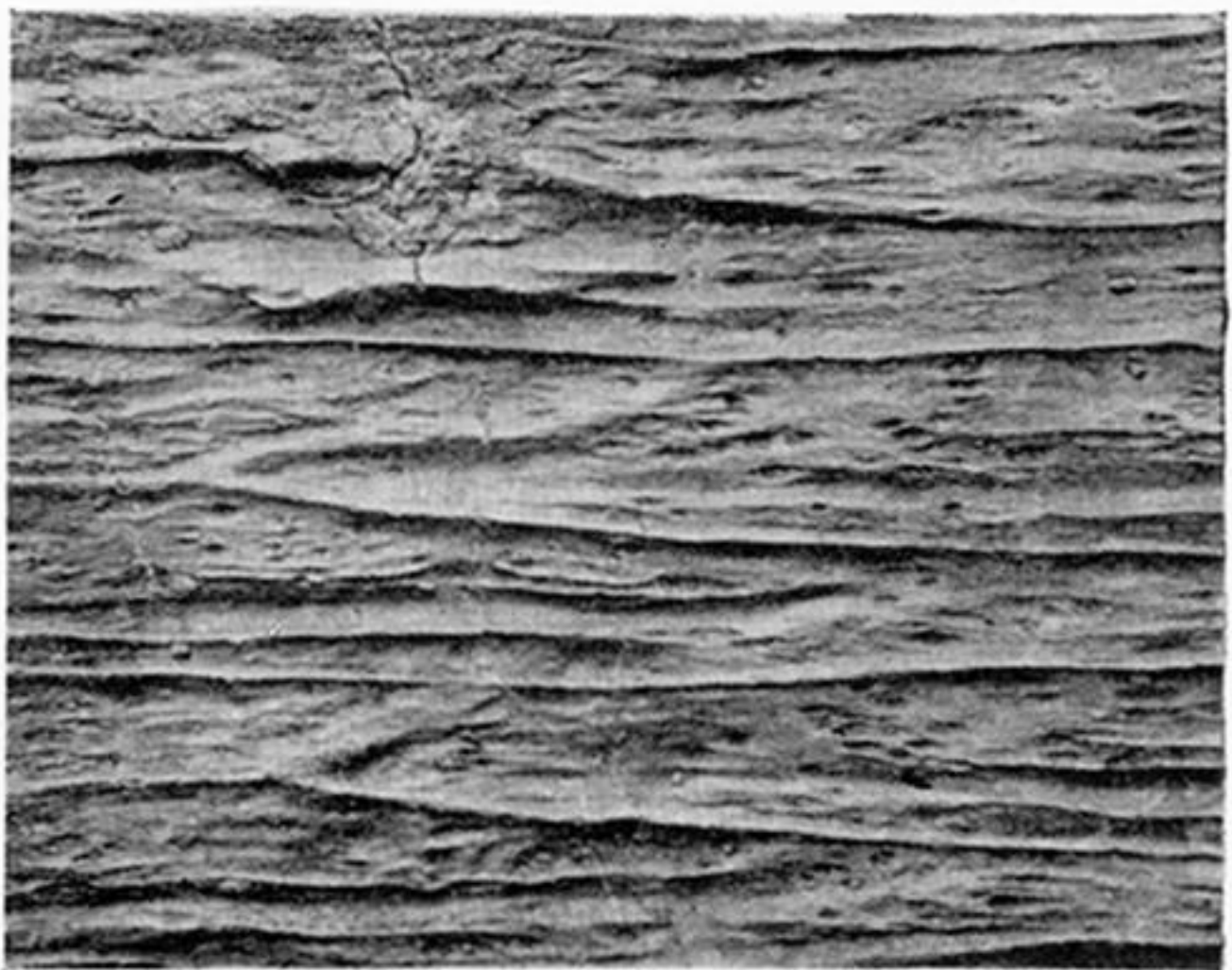
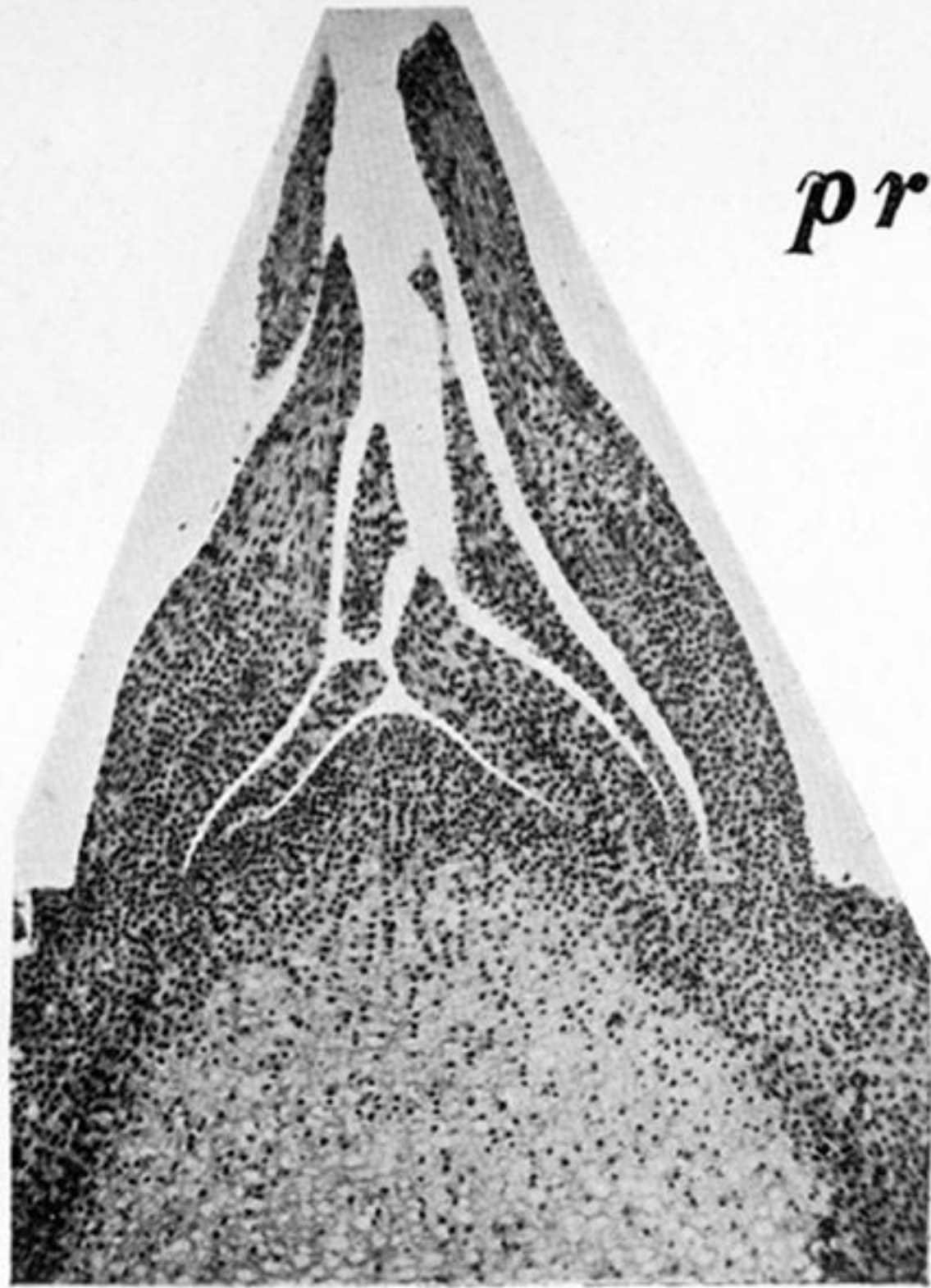


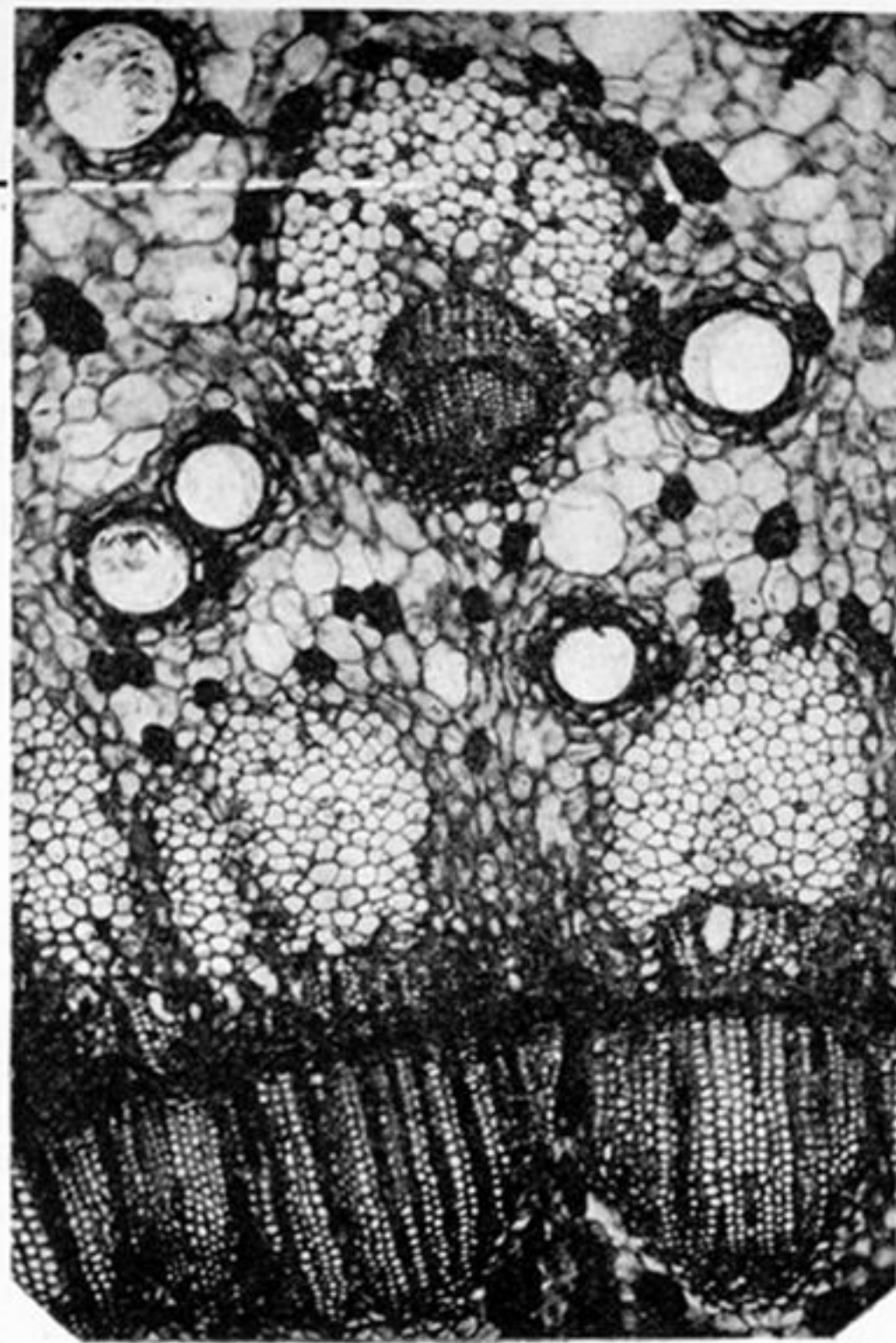
FIG. 6.—*Araucaria imbricata*.



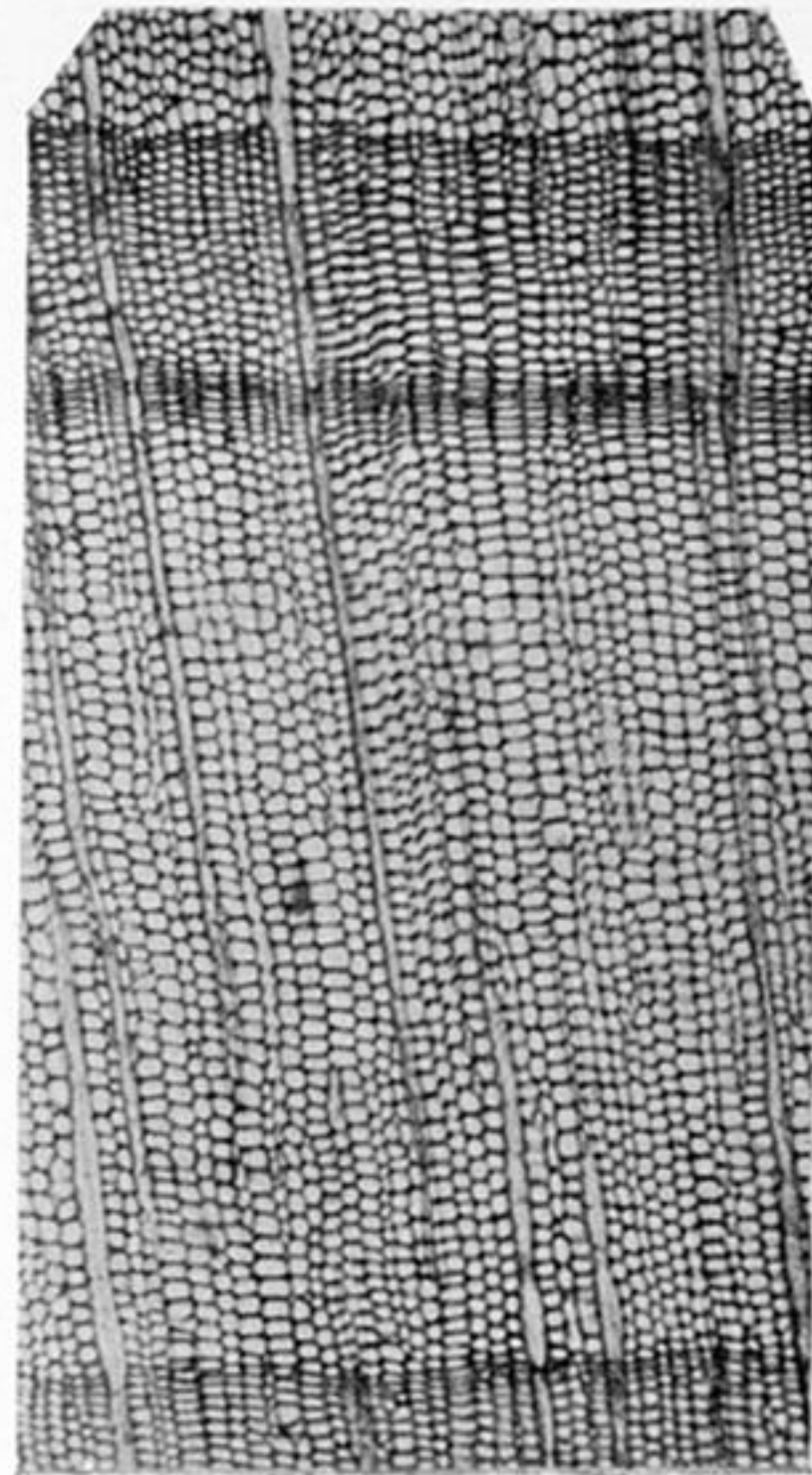


A

*pr*---



B



C

FIG. 17.—*Araucaria imbricata*.



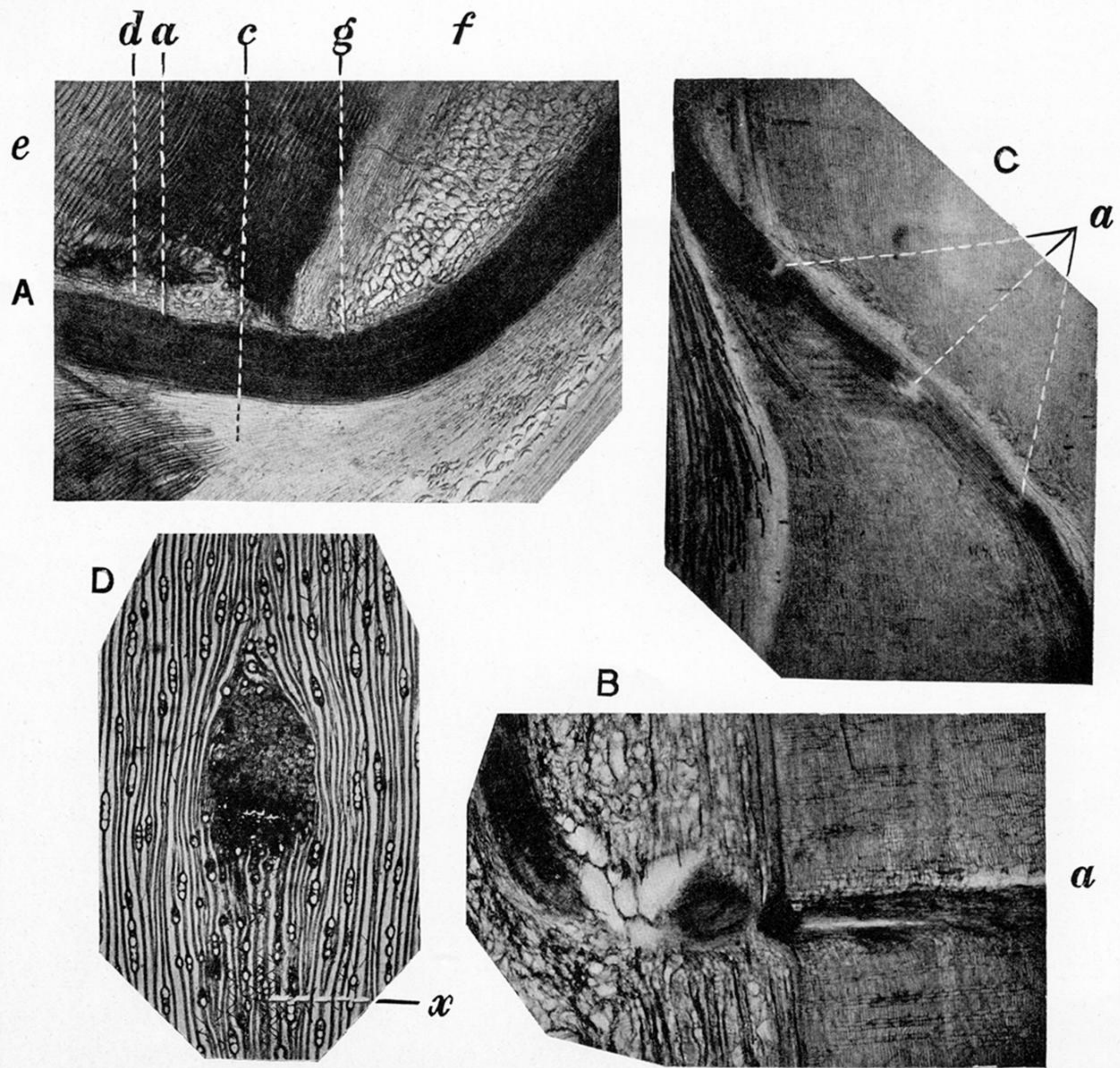


FIG. 21.—A, B, D, *Araucaria imbricata*. C, *Agathis robusta*.